THE MORPHOLOGY OF SOME MITRIFORM GASTROPODS WITH SPECIAL REFERENCE TO THEIR ALIMENTARY AND REPRODUCTIVE SYSTEMS (NEOGASTROPODA)

W. F. Ponder [1]

Dominion Museum, Wellington, New Zealand

ABSTRACT

The alimentary canal and reproductive systems of *Strigatella paupercula* (Linnaeus), *Austromitra rubiginosa* (Hutton) and *Peculator hedleyi* (Murdoch) are described in detail and compared with those of several allied species. The main features of the head-foot, pallial cavity, renal organ and circum-oesophageal ganglia are briefly indicated.

The species described fall into 3 families, the Mitridae, Vexillidae and Volutomitridae, each family having a very distinctive type of alimentary canal. A peculiar epiproboscis, present in the proboscis of the Mitridae, serves as a vehicle for the salivary ducts. Accessory salivary glands and a gland of Leiblein occur in the Vexillidae and the Volutomitridae, but are both absent in the Mitridae. Whereas the alimentary canal of the Vexillidae and Volutomitridae have several features in common, their genital tracts are quite distinct. The reproductive structures in the Vexillidae and Mitridae are very similar. Common features of the species considered include an anal gland, columellar plaits and lack of an operculum, as well as an overall similarity of their shells, features the author considers to be of secondary importance in assessing their relationships at the family level. Other features of the Mitridae (s. s.) not found in the other 2 families include a purple hypobranchial secretion, vase-shaped egg capsules, and a ventral pedal gland in the female. The egg capsules of *Austromitra* and *Microvoluta* are hemispherical. The renal organ has the primary and secondary lamellae in separate areas in the Mitridae, but they are interdigitated in the other 2 families. There do not appear to be any significant differences in the circum-oesophageal ganglia of the 3 groups.

INTRODUCTION

The mitrids have long been objects of curiosity and pleasure to conchologists and their colourful shells are often prized in collections of Indo-Pacific molluscs. Very little, however, is known of the morphology of these animals which are classically placed together in 1 family and are distinguished by their heavy, often small shells with strong columellar folds and relatively small apertures.

Cernohorsky (1966, 1970) and Coan (1966) have recently reviewed the genera of the family Mitridae which, according to Cernohorsky, is composed of 4 sub-families in which are included about 500 Recent species.

The mitrids, as a group, are found most abundantly in the Indo-Pacific region, although many species are known from other areas. Some species inhabit rocky shores or coral reefs where they nestle under boulders or coral blocks, or in crevices, whereas others burrow in sand. The biology of the vast majority of mitriform gastropods is very poorly known and practically no information is available on their feeding habits.

---

[1]Present address: Australian Museum, Sydney, Australia.

The first account of mitrid anatomy is that of Quoy & Gaimard (1833) on the gross anatomy of *Mitra mitra* (Linnaeus) (=*episcopalis* Linnaeus) and the external features of several species. Vayssière (1901) described the structure of the proboscis of *Mitra zonata* Marryatt, and later (1912) the external features of the living animal. The first work of importance, however, was that of Risbec (1928) who described various aspects of the morphology of 5 species of mitrid. These included *Mitra scutulata* (Gmelin) (=*Strigatella scutulata*), *M. crenulata* (Gmelin) (=*Pterygia crenulata*), *M. retusa* Lamarck (=*Strigatella retusa*), *M. microzonias* Lamarck (=*Pusia* sp., probably *P. consanguinea* Reeve), and *M. luculenta* Reeve (=*Vexillum luculentum*). In 1955 Risbec compared *Vexillum hebes* (Reeve) with these species. Cernohorsky (1965, 1966) and Cross (1967) described the living animal of some species and made brief mention of some of their habits. Cernohorsky (1970) briefly reviewed the anatomy of the group. Cate (1968) gave an account of the mating behaviour of *Mitra idae* Melville and its egg capsules. Egg capsules have also been described for *Strigatella scutulata* (Habe, 1944), *Mitra astricta* Reeve and *Strigatella auriculoides* (Reeve) (Ostergaard, 1950) and *M. filaria* (Linnaeus) (Cernohorsky, 1966). Cernohorsky (1970) described the egg capsules of 4 additional species. The radulae of the mitrid gastropods have received special attention from Troschel (1868-1869), Cooke (1920), Peile (1922, 1936, 1937), Barnard (1959), Azuma (1965), Cernohorsky (1966, 1970) and Cate (1967).

Risbec (1928) and Quoy & Gaimard (1833) have commented on the difficulty of dissecting these animals. Their very thick shells, into which the animal retracts to a considerable degree, make it very difficult to extract an undamaged specimen.

In the present study the anatomy of *Strigatella paupercula* (Linnaeus), *Austromitra rubiginosa* (Hutton) and *Peculator hedleyi* (Murdoch) are described and, where material was available, compared briefly with allied species. Particular stress is given to the morphology of the alimentary canal and reproductive systems, but the main features of the head-foot, pallial cavity, circum-oesophageal ganglia and renal organ are also briefly outlined. Because of the lack of anatomical and cytological information about this group most of the information available to the writer is presented in this account.

The main object of this study was to provide a firmer basis for familial classification of the mitriform gastropods on anatomical grounds.

The terminology used here follows Carriker (1943) for the proboscis and its associated structures and Fretter (1941) for the genital systems.

None of the shells of the species described are figured as in each case adequate illustrations can be readily found elsewhere in the literature as indicated. Representative specimens of the material used in these observations are housed in the Dominion Museum.

MATERIAL AND METHODS

The localities from which material was collected are mainly in New Zealand and the New Hebrides, S.W. Pacific Ocean. More detailed collection data are entered preceding the description of each species. Specimens were fixed for histological examination in Bouin's fluid. Material was double embedded by Peterfi's celloidin-paraffin method (see Pantin, 1962) and sections were cut at 7-9 μ and stained with Mallory's triple stain. Other specimens were dissected after fixation in Bouin's fluid, formalin or after preservation in alcohol and, in some cases, dissected alive.

PART 1

STRIGATELLA PAUPERCULA
(Linnaeus)

1758 *Voluta paupercula* Linnaeus, Syst. Nat. ed. 10, p 731.

1965 *Strigatella paupercula*; Cernohorsky, Veliger, 8: 112, pl. 17, fig. 59.

A full synonymy and description of the shell of this species is given by Cernohorsky (1965), and the radula is also described by that author (1966). The material used for the following account was collected at Port Vila, Éfaté Island, in the New Hebrides, in January, 1967. The species was abundant in the upper part of the shore where they clustered in crevices amongst coral blocks.

The rather short foot is dark-brown above, and has a white sole. The snout, siphon and tentacles are white distally, and dark brown proximally. A long slit across the anterior edge of the foot forms the opening to the anterior pedal gland. In female specimens a broad, white, transverse strip runs down the right side of the foot from the pallial cavity, and anteriorly, a small ventral pedal gland is present. A columnar epithelium covers the foot above where it is cuticulate and the distal halves of the epithelial cells are filled with pigment granules. The ciliated sole epithelium is thicker, and rich in mucous cells.

The long pallial cavity contains a very large, brown osphradium and a slightly longer ctenidium on the left side, and a narrow, thick hypobranchial gland is wedged between the ctenidium and the gonoduct. This gland has a smooth internal surface and in life produces a purple secretion similar to that seen in some other mitrids (Cernohorsky, 1965). The much larger *Mitra mitra* has the hypobranchial gland pleated as in *Buccinum* (Dakin, 1912) and *Alcithoe* (Ponder, 1970), and also produces a purple fluid that stains the hands and has a pungent odour (Quoy & Gaimard, 1833). The ctenidial filaments are triangular, with the width of their bases slightly less than their height. The curved osphradium has about 40 filaments on its concave lower (left) side and 70 on its upper side.

No close study was made of the circulatory, renal, or nervous systems, although it was noted that the renal organ has a very similar structure to that of Perrier's (1889) "méronéphri-

diens," with the primary and secondary glandular lamellae separated. The circum-oesophageal ganglia show a marked concentration, and are of the normal rachiglossan pattern (Fig. 6H).

The Alimentary Canal

The most conspicuous feature of the alimentary canal is the massive proboscis. The external shape of this structure has been indicated in several species by Quoy & Gaimard (1833), who also gave a brief description of its morphology in *Mitra mitra*. Vayssière (1901) described the internal structure of the proboscis of *Mitra zonata*, as did Risbec (1928) in the species that he examined. All of these authors commented on the prominent and unique structure of the mitrid (s.s.) proboscis which has generally been regarded as a poison gland (Risbec, 1928; Thiele, 1929; Cernohorsky, 1965, 1966). It was referred to as a "tongue" by Quoy & Gaimard (1833) and as a protractile organ by Vayssière. The present investigation shows that there is no glandular tissue in this structure and that it is in fact a muscular rod that acts as a vehicle for the salivary ducts. To avoid ambiguity a new term, epiproboscis, will be used here.

The Proboscis. In preserved material the pleurembolic proboscis measures up to about $^2/_3$ of the length of the shell when extended and as little as 1.6 mm when fully retracted. The wrinkled appearance of the extended organ shows that it is capable of further elongation. Retraction of the proboscis, as revealed in preserved material, is achieved in 2 ways, although it is probable that 1 of these may be due to an unnaturally violent contraction brought about by contact with the preserving fluid. Specimens preserved in alcohol usually have the proboscis irregularly folded into the proboscis sac. Its walls are heavily pleated and its overall diameter is only slightly greater than the average diameter of the protracted organ. Practically none of the proboscis wall is inverted to form part of the proboscis sac. In formalin-fixed material the pro-

boscis was usually considerably short-
ened and showed a subsequent increase
in diameter to nearly twice that of the
extended organ (Fig. 9A). The longitu-
dinal muscle layers in the wall were
correspondingly thicker due to the severe
and possibly unnatural contraction and
much of the basal part of the proboscis
behind the epiproboscis was inverted to
form part of the proboscis sac. Many
specimens preserved in alcohol still had
the proboscis extended, thus suggesting
a sluggish withdrawal similar to that
mentioned by Quoy & Gaimard (1833) in
Mitra mitra.

The proboscis sac is very thin-walled
and spacious. When filled with the re-
tracted proboscis it causes the roof of
the cephalic cavity to bulge into the ante-
rior half of the pallial cavity. A wide,
powerful series of muscles, continuous
with the inner longitudinal layer of the
proboscis wall, run to the floor of the
cephalic cavity and become confluent
with the columellar muscle, whereas 2
lateral muscles with a similar origin,
attached to the roof of this cavity, make
up the main proboscis retractor muscles.
A powerful sphincter muscle guards the
small rhynchostome (opening to the pro-
boscis sheath) through which the unpig-
mented proboscis is everted.

The rather thin proboscis wall con-
sists of an outer layer of circular
muscles, which are sharply separated
from a thicker, inner layer of longi-
tudinal fibres. A basement membrane
lies beneath the outer cuticularized cu-
boidal epithelium.

Sections through the buccal mass and
the middle part of the proboscis can be
seen in Figs. 1B, C, and a lateral view
of the anterior region of the proboscis
in Fig. 1A. The mouth is overhung by
an outer muscular rim, the peristomal
rim (p.r) which is very similar to that
in the muricacean *Urosalpinx cinerea*
(Say) (Carriker, 1943). Short, powerful
muscles (p.r.m) control this rim and
have their origin in the proboscis wall.
It does not appear that this rim can be
flattened to expose the mouth completely,

so that it may function, therefore, as a
sucker or a cushion. Running between
the mouth and the buccal cavity is a
ring of weaker oral retractor (o.r)
muscles. The oesophagus is loosely
bound to the proboscis wall by thread-
like buccal tensor muscles which become
heavier and much more abundant around
the buccal cavity.

The buccal wall is composed of a
thick mass of circular muscles and a
superficial layer of longitudinal ones,
whereas its lining epithelium is covered
ventrally with stout cuticle over which
the odontophore moves. Bordering this
thick cuticular plate are the anterior
extensions of the dorsal folds (d.f).

The odontophore (Fig. 2A) is pink in
life, short and wide, and covered dor-
sally by a thin sheet of transverse mus-
cle (Fig. 1B; d.t.m). Wide odontophoral
cartilages (od.c) extend the length of
the odontophore and come close together
in front, although they do not join. The
triangular, dorsal subradular membrane
protractor muscles (d.sm.p) are at-
tached to the ventral edge of the ante-
rior portion of the cartilages and to the
radular sac. Below these muscles lie
the large dorsal subradular membrane
retractor muscles (d.sm.r) which are
attached to the inner ventral edges of
the cartilages along the posterior $^2/_3$ of
their length. As well as being fixed to
the subradular membrane these muscles
are fixed to the radular sac. The odonto-
phoral protractor muscle sheets (l.p.od)
lie laterally, being inserted in the poste-
ro-lateral buccal wall, and run to the
posterior end of each cartilage. Below
these muscles lie the lateral subradular
membrane retractor muscles (l.sm.r)
which are attached to the dorsal edge of
each cartilage, and to the subradular
membrane after passing around the ven-
tral edge of the cartilages. Lying below
and near the anterior end of the odonto-
phore, and attached to the anterior end
of the odontophoral cartilages from
where they pass into the latero-ventral
wall of the buccal cavity, is a pair of
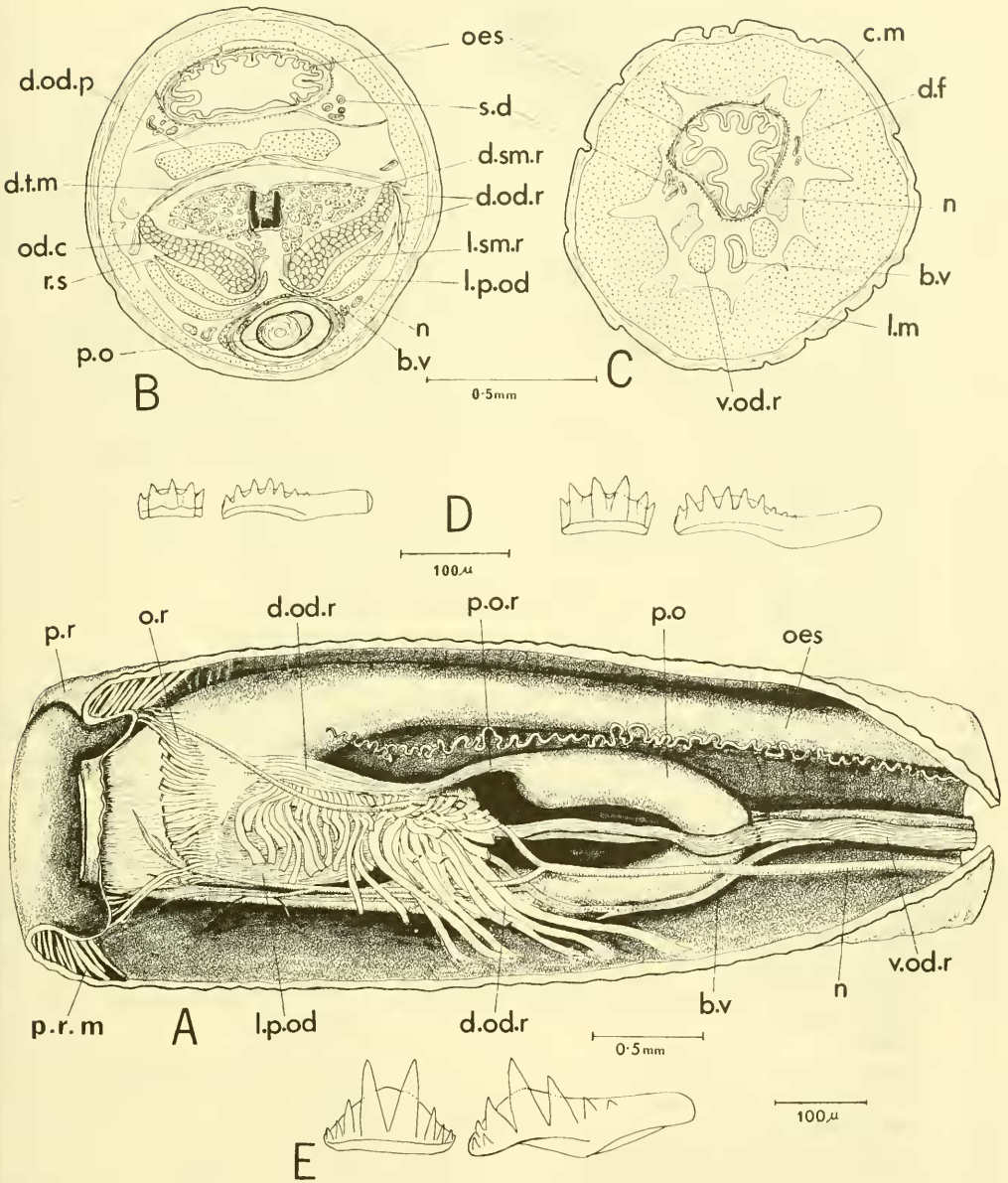short, odontophoral divaricator muscles.

FIG. 1. A–D. *Strigatella paupercula* (Linnaeus): A. Lateral view of the anterior end of the proboscis opened from the left side; B. Transverse section of the proboscis through the odontophore; C. Transverse section of the proboscis behind the epiproboscis; D. Radular teeth from 2 specimens from Port Vila, Éfaté Island, New Hebrides, showing variation. E. *Imbricaria conovula* (Quoy & Gaimard). Radular teeth (Port Meslep, Éfaté Is., New Hebrides).

A transverse muscle (t.m) runs ventrally between the anterior portions of the odontophoral cartilages to which it is attached. A series of short, dorsal odontophoral retractor muscles (d.od.r) are fixed to the odontophoral cartilages along the posterior $2/3$ of their length, their area of attachment coinciding with

KEY TO LETTERING ON FIGURES

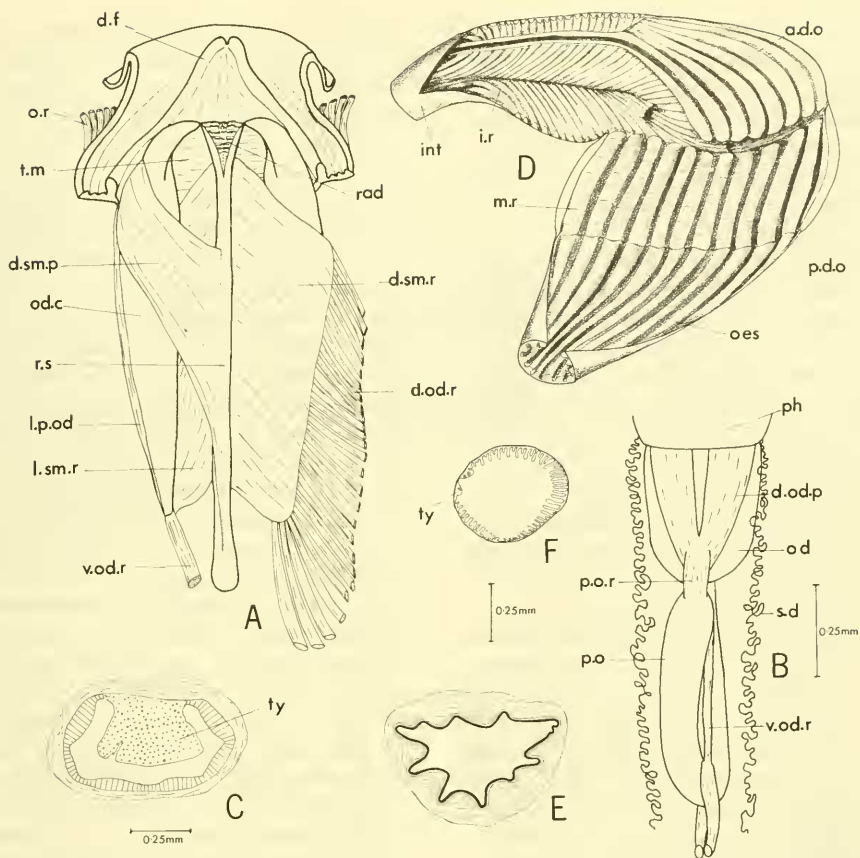|			
a	anus	od.	odontophore
a. d. o	opening to anterior digestive gland duct	od. c	odontophoral cartilage
		od. r	odontophoral retractor muscle
a. g	anal gland	oes	oesophagus
alb	albumen gland	o. l. m	outer longitudinal muscle strip
a. s. d	accessory salivary gland duct	op.	operculum
a. s. g	accessory salivary gland	o. r	oral retractor muscle
a. v. l	antero-ventral lobe of capsule gland	o. t	oral tube
b	buccal ganglion	o. t. r	oral tube retractor muscle
b. a	pale blue staining area of capsule gland	p	pleural ganglion
		p. a	purple-staining area of capsule gland
b. c	bursa copulatrix		
bl. c	blue-staining gland cells	pal. o	pallial opening of oviduct
b. v	blood vessel	p. d	gonopericardial canal
c	cerebral ganglion	p. d. o	opening to posterior digestive gland duct
cae	caecum of stomach		
cap	capsule gland	ped	pedal ganglion
c. d. o	common opening of digestive gland ducts	pen	penis
		ph	buccal cavity
c. m	circular muscle	p. gr	penial groove
c. r	ciliated region	pn. d	penial duct
d. c	dorsal channel	p. o	epiproboscis
d. f	dorsal fold	p. oes	posterior oesophagus
d. g. l	duct of gland of Leiblein	p. o. r	epiproboscis retractor muscle
d. od. p	dorsal odontophoral protractor muscle	p. o. s	epiproboscis sheath
d. od. r	dorsal odontophoral retractor muscle	p. r	peristomal rim
d. sm. p	dorsal subradular membrane protractor muscle	pr.	prostate gland
		pr. c	prostatic cells
		p. r. m	peristomal rim muscles
d. sm. r	dorsal subradular membrane retractor muscle	pr. o	pallial opening of prostate
		p. s	proboscis sheath
d. t. m	dorsal transverse muscle	r	rectum
e. d	ejaculatory duct	rad	radula
g. c	gland cells	r. c	red-staining gland cells
g. l	gland of Leiblein	rh	rhynchostome
i. d	ingesting gland duct	r. m	radial muscle
i. g	ingesting gland	r. s	radular sac
int	intestine	sb. o	sub-oesophageal ganglion
i. r	intestinal region of stomach	s. d	salivary duct
l. f	left fold of ventral channel	s. g	salivary gland
l. m	longitudinal muscle	s. gr	seminal groove
l. p. od	lateral odontophoral protractor muscle	sp	sperm
		sp. o	supra-oesophageal ganglion
l. sm. r	lateral subradular membrane retractor muscle	s. s	supporting sheath
		s. v	seminal vesicle
m. a	mucous secretion area of capsule gland	tes	testis
		t. m	transverse muscle
m. c	mucous cells	ty	typhlosole
m. o	glandular epithelium of the section of the mid-oesophagus behind the valve of Leiblein	va	vagina
		v. c	ventral channel
		v. l	valve of Leiblein
m. r	muscular region of stomach	v. od. r	ventral odontophoral retractor muscle
n	nerve		
o. a	orange-staining area of capsule gland	vest	vestibule

FIG. 2. *Strigatella paupercula* (Linnaeus). A. A schematic diagram of the odontophore and the epiproboscis and its associated muscles viewed dorsally. B. Dorsal view of the buccal apparatus showing the epiproboscis and its associated dorsal muscles. C. Transverse section of the posterior part of the mid-oesophagus to show the "typhlosole". D. The stomach opened dorsally. E. A transverse section of the muscular portion of the stomach. The cuticle lining is shown in black. F. A transverse section of the intestinal region of the stomach.

TABLE 1. Radula variation in *S. paupercula*

Cusp formula on central tooth	Width of central tooth in microns	Number of cusps on lateral teeth (excluding indistinct denticles)
2-1-2	62	9
2-2-3	85	9
2-2-2	40	5
2-1-2	59	6
2-1-2	50	4
2-1-2	42	5

All specimens from Port Vila, Éfaté Is.

the insertion of the dorsal subradular membrane retractor muscle (d.sm.r). The former muscles radiate dorsally and ventrally and slope obliquely backwards before becoming attached to the proboscis wall. The posteriorly placed strands of this muscle are longer and a little heavier than those in front. A pair of narrow, ventral odontophoral retractor muscles (v.od.r) are fixed to the posterior end of the odontophoral cartilages, and extend back through the

proboscis to eventually anchor themselves in the floor of the cephalic cavity. In addition, a pair of thin, broad, ventral odontophoral protractor muscles lie below the odontophore and are fixed to the floor of the buccal cavity in front, and to the posterior ends of the odontophoral cartilages behind.

The radular sac (r.s) is only slightly longer than the odontophore and opens out in the usual manner just before bending downwards over the anterior ends of the odontophoral cartilages. The worn radular teeth are presumably loosened by the subradular membrane, being resorbed in the ventral pocket at the distal end of the radula. A thin strip of muscle runs backwards from this distal pocket and is attached to the ventral surface a little in front of the proximal end of the radular sac.

The radula of *Strigatella paupercula* has been described by Cernohorsky (1966, p 110, fig. 17) but comparisons of the radulae of several specimens (see Table 1) has shown that an unusual amount of variation exists (Fig. 1 D). Peile (1936) has also shown radular variation in *Mitra cucumerina* (Lamarck).

The salivary ducts (s.d) are narrow convoluted tubules which lie alongside the oesophagus and, just before the oesophagus opens into the buccal cavity, they enter its walls to lie beneath the dorsal folds in the usual manner. However, instead of opening into the buccal cavity, they pass ventrally as exceedingly fine ducts which merge just above the thin-walled sheath of the epiproboscis (Fig. 3).

The Epiproboscis. This muscular rod is the most conspicuous feature of the buccal mass (Figs. 1A, 3, 9A). It gradually tapers anteriorly and when retracted forms an introvert which lies in a sheath (p.o.s) beneath and behind the buccal mass with its posterior portion arching up to the end of the buccal mass. Thus the epiproboscis forms a U behind, and about 1 $\frac{1}{2}$ times the length of, the odontophore. It is translucent yellow in life with smooth, glossy walls, and is at-

tached to the odontophore just above the end of the radular sac by a short, bulky retractor muscle (p.o.r). This in turn is fixed to the base of a pair of powerful dorsal odontophoral protractor muscles which (Figs. 1A, B; 3B; d.od.p) are incorporated in the wall of the buccal cavity and lie on the dorsal surface of the odontophore where they meet. These muscles appear to have no homologues in other neogastropods.

The whole of the U-shaped portion of the epiproboscis lies loosely in the proboscis cavity, except where it passes through the 2 ventral odontophoral retractor muscles (v.od.r) to which the epiproboscis sheath is loosely bound on its inner (anterior) face by a transverse muscular connection. It is this connection, and the posterior continuation of the ventral odontophoral retractors that Risbec (1928) refers to as a "horse-shoe shaped muscle", although it could more appropriately be termed hairpin-shaped. It appears as though this modification of the odontophoral retractor muscles serves to aid in the retraction of the epiproboscis in harmony with the rest of the buccal mass. It is not essential in the manipulation of this organ however as its absence is noted in *Pterygia crenulata* (Risbec, 1928) and *Imbricaria* spp. (herein).

The structure of the epiproboscis is shown in Fig. 3. Throughout most of the posterior U-shaped portion (Fig. 3), the retracted organ is composed of an outer sheath containing an external longitudinal layer and an inner layer of circular fibres. The inner surface of the ventral part of the sheath (Figs. 3b-d) is lined with a very thin epithelium covered with cuticle, but at the bend in the U the epithelium crosses the gap between organ and sheath and becomes confluent with the epithelium of the nonintrovertible part of the epiproboscis, which is thus, also, naked behind this point (Fig. 3a). The epiproboscis has a central core of longitudinal muscle (l.m) which is surrounded by circular muscles. The circular muscle is thick distally,
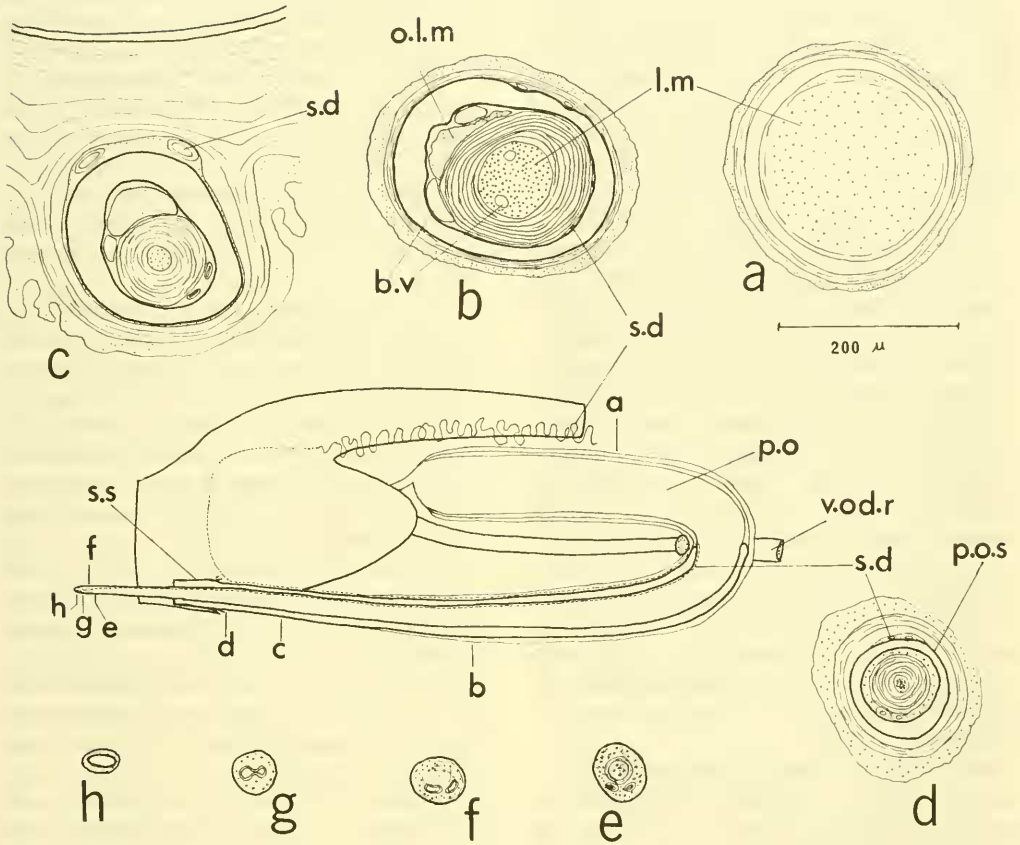
FIG. 3. *Strigatella paupercula* (Linnaeus). Semi-diagrammatic lateral view of the buccal apparatus and the epiproboscis. The positions of the sections a-h are indicated. a-h sections of epiproboscis (see text).

but longitudinal muscles predominate in the dorsal arm of the U. A strip of longitudinal muscle fibres (o.l.m) lies dorsally along the whole ventral arm of the retracted epiproboscis and has its origin in the posterior mass of longitudinal muscle fibres. This muscle probably serves to bend the organ, while the circular fibres cause it to elongate and the central longitudinal muscle core withdraws it. Small blood spaces (b.v) lie beneath the epithelium and these would supply the turgor necessary in protraction. The sheath remains disconnected from the buccal mass almost to its opening below the mouth where it is fixed to the outer integument by a few muscle fibres. The combined outer

integument and sheath can form a short cone (s.s) which projects forwards and surrounds a portion of the epiproboscis, thus acting as a supporting sheath. Below the buccal mass the sheath has very thin walls composed only of the epithelium and a few longitudinal muscle fibres, but below the buccal cavity it is enclosed by a muscular tunnel of longitudinal fibres (Fig. 3c, d).

The salivary ducts (s.d) run on the upper side of the sheath, just inside the epithelium, to the bend in the U where, along with the epithelium, they cross to the non-invaginable portion of the epiproboscis. They then extend, as exceedingly fine ducts, along this organ (Figs. 3b-e) until, just behind its tip, they become embedded in a mass of connective tissue and scattered longitudinal fibres (Fig. 3f). Here they expand and become confluent (Fig. 3g) and the combined duct opens at the tip of the organ, appearing to be an invagination of the outer epithelium at this point (Fig. 3h).

The epiproboscis thus functions as an extensile vehicle for the salivary ducts. It is likely that the saliva is administered only in small amounts. The ducts are very long and narrow, without cilia or peristaltic muscles to aid the delivery of the secretion.

On extension the epiproboscis is inverted at its posterior end and the retractor muscle becomes surrounded by the outer sheath. Only partial inversion, up to the point where the hairpin muscle is joined to the outer sheath, was observed. Further protraction probably includes the incorporation of the ventral odontophoral protractor muscle into the longitudinal core of this organ. Thus retraction of the epiproboscis is probably a 2 stage process, the first being achieved by the withdrawal, by its contraction, of the ventral odontophoral retractor muscle from the introvert, and the second by using this muscle as a pivot, by the contraction of the epiproboscis retractor muscle.

The Oesophagus. The anterior oesophagus (Fig. 1, oes) is adapted for the passage of large pieces of food. It is a wide, oval tube with low, longitudinal ridges. Above the odontophore the laterally placed dorsal folds (d.f) are readily distinguishable but they become indistinguishable in the posterior portion of the anterior oesophagus which is nearly circular in section. The short, ciliated epithelium has abundant mucous goblet cells, although these are more sparse ventrally in the anterior portion which lies above the buccal mass. The oesophageal wall is rather thin and consists of a few outer longitudinal muscle fibres and an inner circular muscle layer.

A pair of oblique, glandular pads which are inclined forwards from the dorsal surface lie just in front of the nerve ring and represent the valve of Leiblein. They are lined with tall mucous cells of the same type as those occurring in the valve of Leiblein of other neogastropods. There is no definite indication of torsion such as occurs in some other rachiglossans (Graham, 1941). The anterior oesophageal ridges, however, terminate at the glandular pads and are inclined a little to the right, but, as the dorsal folds are not distinguishable at this point, and there is no distinct ventral groove, no further direct indication of torsion could be observed. There are, however, mid-dorsally in the mid-oesophagus, a pair of somewhat more prominent ridges which have a non-ciliated groove between them. These ridges are covered with a slightly taller epithelium than the rest of the mid-oesophagus and are more richly supplied with mucous cells. They probably represent the dorsal folds in their post-torsional position. Before the oesophagus leaves the nerve ring, a peculiar swelling (Fig. 2c), resembling a short typhlosole, appears in the mid-dorsal line and is bordered on either side by the low dorsal folds. These folds cease at the commencement of the posterior oesophagus immediately behind the swelling. The swelling which consists of an irregular cluster of small

cells was observed in all 12 sectioned specimens, and in dissected material. It is sited where the gland of Leiblein normally opens. That gland is absent in this species, and the function of the swelling is obscure. The remainder of the mid-oesophagus is weakly ridged and is lined with short, ciliated cells, and mucous cells.

Behind the nerve ring the oesophagus rapidly increases in diameter and forms a wide storage crop behind the cephalic cavity. The narrower anterior section has tall, longitudinal ridges covered with short, columnar cells with pale cytoplasm and dense, red staining nuclei. These cells bear short cilia, and mucous cells are abundant. At the end of the pallial cavity the oesophagus narrows a little below the posterior pallial floor. Here it is buried in dense connective tissue, and the epithelium changes to weakly ciliated cuboidal cells having dense cytoplasm and large central nuclei with prominent nucleoli. Occasional large goblet cells occur, but otherwise no glandular tissue is present. In addition the longitudinal ridges become narrower and more irregular than those in front but when the crop is distended with food these flatten out to form a uniformly oval structure. The outer wall of the oesophagus is very thin and composed of only a few longitudinal muscle fibres, and a little connective tissue.

The Salivary Glands. These form a relatively large mass about 0.8 mm in length which lies over the cerebral ganglia. They form a single compact body which can be fairly readily separated into 2 lobes. The cells are of 2 types. One has a bluish staining granular cytoplasm, and the other is filled with purplish-red staining granules. Both types occur with equal frequency and are arranged in narrow, irregular tubules. Although the salivary ducts (Figs. 1B, C; 3; 2B, s.d) have a ciliated pavement epithelium near the glands, they lose this where they come to lie alongside the oesophagus, and have only a wall of fibrous tissue.

The Stomach. The oesophagus opens into a muscular gizzard-like structure with 10-14 longitudinal ridges lined with thick cuticle (Figs. 2D; m.r ; 2E). A thick layer of circular muscle surrounds these ridges which have an epithelium of cuboidal cells. This region of the stomach presumably effects the initial breaking up of the food. As there is no gland of Leiblein the first important digestive enzymes commence the breakdown of the food in the stomach. A small posteriorly pointing area, all that remains of the main gastric lumen, lies between the oesophageal and intestinal arms of the stomach and is lined with columnar cells, the irregular height of which forms low, broad ridges. The opening to the posterior digestive gland (p.d.o) lies mid-ventrally immediately behind the muscular region and a transverse channel runs from this opening across the posterior edge of the muscular area. The anterior digestive gland duct (a.d.o) opens near the inner end of the intestinal region. The intestine (int) emerges from the stomach on the right, above the oesophagus. The intestinal region (i.r) corresponds to the style sac of many prosobranchs. It has numerous, tall ridges running obliquely into a shallow groove, while on the posterior face lies a pair of small folds or typhlosoles (Fig. 2F; ty). These typhlosoles are formed by columnar cells with a few large goblet cells containing refringent secretory masses. The dorsal epithelium of the intestinal region consists of small cuboidal cells with relatively large nuclei, whereas laterally and ventrally the cells are even smaller and flattened.

The Digestive Gland. The large posterior (left) lobe of the digestive gland lies behind the stomach, and the relatively minute anterior (right) lobe in front. Their short ducts are lined with a columnar epithelium continuous with that of the stomach. The digestive cells vary from 50-70 μ in height when mature, and appear to be of 1 type only,

having orange-red-staining granules of irregular size in the mature state. "Immature" cells which lie between the bases of the larger cells have colourless granules, and similar granules occur in the distal borders of mature cells. Some of the digestive cells have weak cilia, but the majority are unciliated. Islands of amoebocytes, containing dark-green refringent granules, are scattered through the digestive gland. Cells similar to these are a common occurrence in the digestive glands of stenoglossans (Smith, 1967).

The Intestine.   The opening to the intestine from the style sac is not guarded by a sphincter muscle but an abrupt change in the epithelium occurs. The intestine curves downwards beneath the renal organ, which encompasses it, before emerging on the right side of the pallial cavity.   A tall columnar epithelium, which contains occasional gland cells, lines the upper intestine, and variations in its height form about 6 low, irregular ridges which differ appreciably from those of the style sac region. As the intestine enters the pallial cavity, red-staining glandular cells suddenly become abundant in its walls. In the middle part of the pallial cavity the gland cells become less numerous and the cilia longer.   This rectal region (Fig. 4A, F; r) has many low folds and continues unchanged to the anus which is placed some distance back from the mantle edge.

The Anal Gland.   As typical of many neogastropods, Strigatella has an anal gland (Fretter, 1946: Smith, 1967). It is composed of 1-4 tubules which extend through most of the right pallial wall (Fig. 4F; a.g). The weakly cilated cells are like those in the anal gland of most other neogastropods and contain brown-staining granules. These granules are accumulated in their distal ends which are eventually nipped off. Amoebocytes with similar granules are found around the bases of the cells. The gland opens just in front of the anus by way of a very narrow, ciliated duct lined with cuboidal cells.

Smith (1967) suggests that amoebocytes carry the granules produced in the digestive gland to the anal gland which then excretes them, and cites as evidence the presence of amoebocytes carrying granules around bases of the cells of the anal gland. In Strigatella, however, the large, dark green-staining granules in the digestive gland amoebocytes are quite different from those in the amoebocytes of the anal gland.

Food.   Fragments of sipunculid worms were found in the crop of several specimens.   Strigatella paupercula has also been observed feeding on sipunculid worms near Honiara, Solomon Islands, by Prof. J. E. Morton (pers. comm.). [After this paper was written, Kohn (1970) reported on the feeding behaviour of Strigatella litterata (Pacif. Sci., 24: 483-486), which also feeds on sipunculids.]

The Male Genital System

The Testis.   The tubules of the testis ramify through the digestive gland, although they are concentrated on the ventral side of the visceral mass. Spermatozoa are collected into a wide, tightly coiled seminal vesicle (Fig. 4A; s.v) which is lined with cells varying from cuboidal to columnar in its upper region. These cells often contain brown spherules and in some areas their distal ends are budded off, these being added to the mass of sperm. Sperm ingestion was observed taking place in some groups of cells that had pseudopodial processes developed on their distal edges.   The anterior coils of the seminal vesicle are wider and lined with pavement epithelium.

The Vas Deferens.   The renal vas deferens has a ciliated epithelium which forms longitudinal ridges and is surrounded by a very thin layer of connective tissue.   There is no sphincter muscle
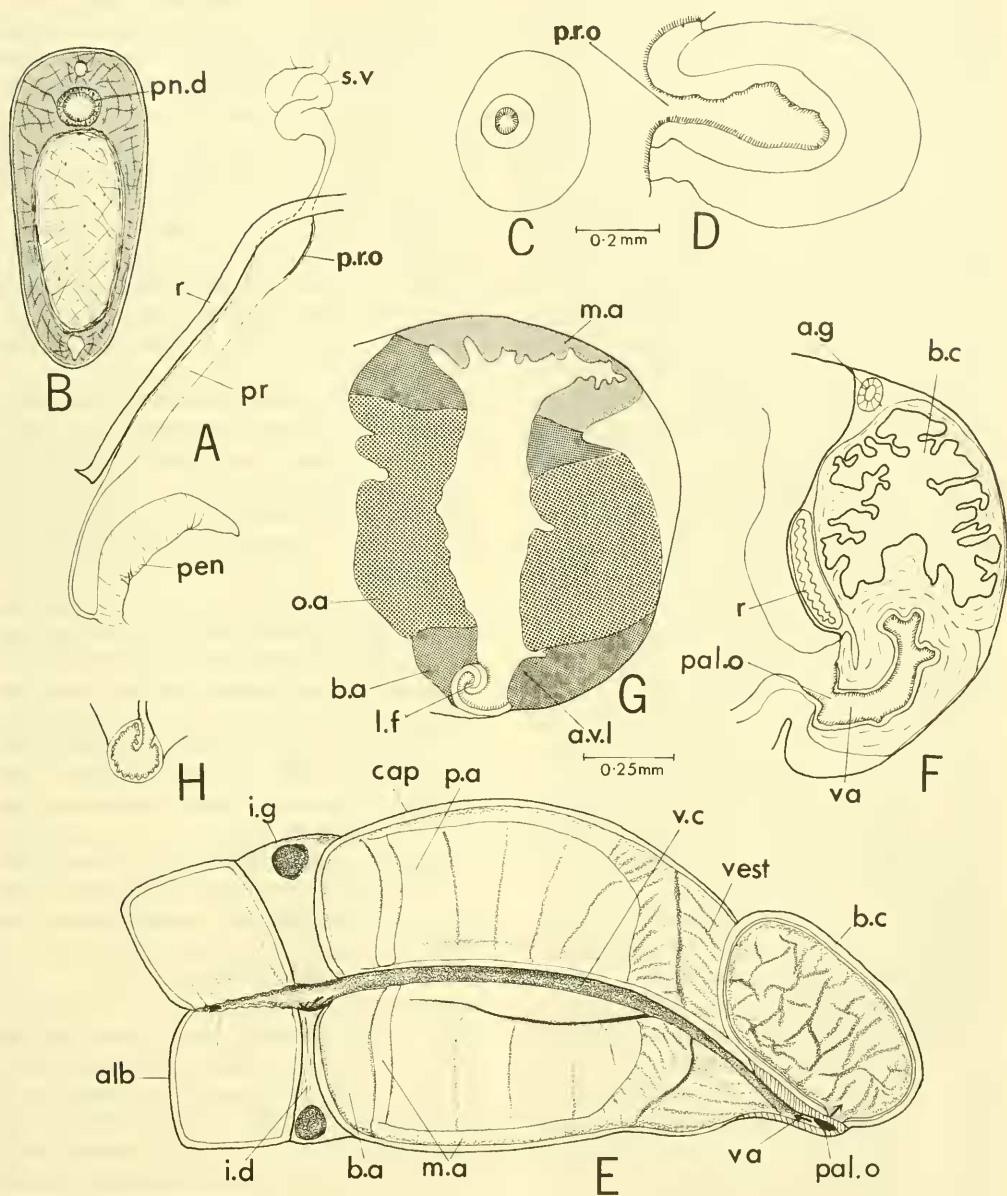
FIG. 4. A-G. *Strigatella paupercula* (Linnaeus): A. The male genital system, excluding the testis
B. A transverse section of the penis; C, D. Transverse sections of the anterior (C) and poste-
rior (D) parts of the prostate gland; E. The pallial oviduct opened dorsally and viewed from the
right; F. A transverse section of the pallial opening of the oviduct and of the bursa copulatrix.
G. A transverse section of the capsule gland. H. *Imbricaria conularis* Lamarck: A transverse
section of the ventral channel.

separating it from the seminal vesicle and no gonopericardial duct, even though it is buried in connective tissue of the pericardial wall.

The Prostate Gland. A prostate gland (pr) commences at the posterior end of the pallial cavity where it receives the vas deferens, and is lined with tall, narrow, ciliated cells with small blue-staining granules and, in addition, a mass of similar staining cells lies below. This posterior portion, which is rather short, is broader than the remainder of the gland, and communicates with the pallial cavity by way of a ciliated slit (Figs. 4A, D; pr.o). The rest of the gland (Figs. 4A, C) has an enclosed duct, and the glandular cells have larger, round nuclei. Their secretory granules stain pale pink. There is no indication of a line of fusion of an originally open groove as seen in some muricids (Fretter, 1941). Nearer the penis the gland becomes narrower and consists of the duct lined with short columnar cells, and a few blue-staining sub-epithelial cells scattered around it. This portion of the male system corresponds to the ejaculatory duct. It is about 150 μ in diameter, with a wide lumen, and continues unchanged bulging from the pallial wall, into the base of the penis.

The Penis. The penis (pen) lies behind the right cephalic tentacle. It is rather elongate when at rest, oval in section, slightly narrower at its base than in the middle region, and tapers to a blunt point. Its outer epithelium consists of small cuboidal cells which are covered with a thin layer of cuticle in the basal portion, but have very short cilia distally. The penial duct (Fig. 4B; pn.d) resembles the ejaculatory duct, apart from being a little narrower, and follows a rather irregular path until it opens at the distal tip of the penis. This duct lies just outside a wide, central area loosely filled with variously orientated muscle fibres and surrounded by a ring of circular muscle. This central area is primarily a blood space and probably plays a major part in the

elongation of this organ. The rest of the penis consists of a mass of connective tissue and muscle fibres in which lie loosely packed, blue-staining cells like those surrounding the ejaculatory duct (Fig. 4B).

The Female Genital System

Risbec (1928) and Quoy & Gaimard (1833) both briefly mention the pallial oviduct of the mitrids they examined, but no detailed account has been given of the reproductive apparatus of any mitrid.

The Ovary. The ovarian tubules of S. paupercula ramify through the digestive gland and tend to occupy most of the upper visceral mass when mature. The eggs are of moderate size (up to 0.3 mm diam.) and are filled with large yolk granules.

The Upper Oviduct. The upper oviduct is a straight tube lined with irregular, non-cilated columnar cells with central nuclei. These become cilated and form longitudinal ridges as the oviduct passes along the wall of the pericardium, but there is no gonopericardial duct. A few muscle fibres surround the walls of this rather short portion of the oviduct which is a little narrower (140-160 μ in diameter) than the upper oviduct. The renal oviduct enters the albumen gland (Fig. 4E; alb) a little in front of its posterior end.

The Albumen Gland. A more or less straight, ciliated channel lies on the floor of the albumen gland and its thick glandular walls have the same type of histology as certain other rachiglossans (Fretter, 1941). This gland is taller than it is long, and its ventral, ciliated channel continues as a short, wide, non-muscular duct into the capsule gland (cap), as the ventral channel of that organ.

The Ingesting Gland. The duct of the ingesting gland (i.d) is a dorsal outgrowth of the duct between the capsule and albumen glands and both are lined with a ciliated, cuboidal eipthelium. This duct arises on the outer (right)

side of the oviduct and opens into the ingesting gland (i.g) dorsally. The upper portion of the duct, about 250 μ wide, is surrounded by a thin muscle layer, absent from the more ventral portion, and contains masses of orientated sperm. The ingesting gland is a spacious cavity divided into 2 lobes by the intervention of its duct. It is lined with large columnar cells very like those seen in most other Neogastropoda (Fretter, 1941). They have yellowish-brown-staining cytoplasm and are 100-200 μ in height. Sperm lie in irregular masses, or in large orientated bundles like those in the upper part of the duct, and are ingested, along with yolk granules, by the epithelium.

The Capsule Gland. The capsule gland (Figs. 4E, G; cap), which occupies most of the pallial oviduct, is oval in section, with thick lateral lobes which have the epithelium organized in the same way as in the rachiglossan species investigated by Fretter (1941). Several glandular regions in the capsule gland are indicated by their different staining properties, although these are variable in extent in different specimens. A pale-blue-staining area (b.a) lies in the posterior region of the gland, this being bordered in front by 2 transverse strips of non-staining mucous cells (m.a) which are followed by a purple-staining zone (p.a). The middle part of the gland (Fig. 4G) has a lateral reddish-orange-staining area (o.a) bordered above and below on both sides by a narrow wedge of blue-staining cells (b.a) and, on the dorsal wall, by a wide strip of colourless mucous cells (m.a). This latter zone is unlike the other glandular areas in being a simple epithelium which is folded into shallow alveoli and has ciliated cells throughout. The other areas have ciliated cells only in the outer layer of columnar epithelium and have thick, multicellular glands lying below. The ventral channel (v.c) is rather wide, lined with a cuboidal, strongly ciliated epithelium 20-25 μ thick and is overhung by a single fold on the left

(l.f). A low ridge on the right (a.v.l) is also distinguishable and is probably homologous with the right fold in *Alcithoe* (Ponder, 1970) and the antero-ventral lobe in *Nucella* (Fretter, 1941). There is no trace of a right ciliated fold. In the anterior part of the capsule gland the dorsal mucous zone migrates downwards to occupy all of the lateral glandular surface at the anterior end of the gland. A ciliated channel lined with blue-staining gland cells only 50 μ high commences in the mid-dorsal line near the anterior end of the capsule gland and rapidly spreads to occupy all of its dorsal wall.

The Vestibule and Vagina. The oviduct narrows in front of the capsule gland and is lined by simple, ciliated, columnar cells and scattered mucous cells. This portion of the oviduct (Fig. 4E; vest) is longitudinally ridged and quite short. It lies on the inner side of the bursa copulatrix and corresponds to the vestibule in the species investigated by Fretter (1941).

The vestibule rapidly narrows until only the ventral channel remains. At this point it is surrounded by a thick layer of circular muscle fibres and becomes the vagina (va). Two dorsal ridges of ciliated cells persist which represent the 2 lateral walls of the vestibule, and they contain occasional large goblet cells. The ventral wall of the vagina is lined with a non-ciliated, pavement epithelium. The interior of the whole structure is only 0.1 mm in diameter.

The short vagina opens into the pallial cavity (Fig. 4F) a little behind the anus, and the gonopore is surrounded by a thick muscular lip covered with small cuboidal cells containing fine, brownish-staining granules and very elongate nuclei. These cells are strongly ciliated and merge with the epithelium of the distal section of the vagina which consists of cells with longer cilia, pale blue-staining cytoplasm, and oval nuclei.

The Bursa Copulatrix. The opening to the bursa copulatrix (b.c) lies above the

gonopore. Its short, ciliated duct is made up of a series of irregularly folded, low muscular ridges which extend, within the bursa, almost to the anterior limit of this organ. These ridges increase in size and gain additional musculature as they approach the inner bursal aperture, but do not extend much behind it. The bursa copulatrix is an oval body, circular in section and about 0.7 mm in diameter in its middle. It commences just behind the anus and its rather thin, but muscular, walls contain both longitudinal and circular fibres. The lumen is subdivided by a number of irregular lamellae which are penetrated by muscle fibres and lined with small, dense, cuboidal cells covered with cuticle. Occasionally it is packed with orientated and unorientated sperm, the former attached by their heads to the cuticle. This structure thus presumably acts as a sperm receiving organ.

The Pedal Gland. A small ventral pedal gland is present but is not obvious in preserved material. It is a deep depression situated a little behind the anterior edge of the foot and has 3-4 layers of red-staining subepithelial gland cells clustered above the pedal epithelium which is, in this region, a little shorter than that over the rest of the sole.

IMBRICARIA SPECIES

Imbricaria conularis (Lamarck)
1811 *Mitra conularis* Lamarck, Ann. Mus. Hist. Nat., 17, p 219.
1965 *Imbricaria conularis*; Cernohorsky, Veliger, 8: 154, pl. 23, fig. 131, text fig. 11.

Material was collected at Port Havannah, Efate. Is., New Hebrides, on sandstrewn coral rock just below low tide.

Imbricaria conovula (Quoy & Gaimard)
1833 *Mitra conovula* Quoy & Gaimard, Voy. Astrolabe, Zool., 2: 655, pl. 45b, figs. 18-22.
1963 *Imbricaria conovula*; Cate, Veliger, 6: 41, pl. 8, figs. 55-56.

Material collected at Meslep, Éfaté Is., New Hebrides, just below low tide on coral sand.

All of the specimens were, unfortunately, in a fairly fragmentary state owing to the difficulty of removing the animal from the shell without damage. Four specimens of *I. conularis* were sectioned and 1 of *I. conovula* was dissected.

The external appearance of the living animal and the radula of *I. conularis* have been described by Cernohorsky (1965, p 155). The animal differs from *Strigatella* species in not having the dorsal side of the foot heavily pigmented and in details of the radula. The absence of considerable head-foot pigmentation was also noticed in *I. conovula* and in *Mitra* species.

The mantle cavity is similar to that of *Strigatella* and although the overall plan of the alimentary canal and reproductive systems is very similar, there are some differences. The proboscis has only been observed in the retracted state, in which it is relatively wider and shorter than in *Strigatella* and a greater development of the retractor muscles and thickness of the proboscis walls are apparent. The buccal mass, which is contained within the fully retracted proboscis in *Strigatella*, protrudes into the cephalic cavity in *Imbricaria* (Fig. 9C) and the much longer epiproboscis is loosely folded behind. This organ is attached to the posterior end of the odontophore by several thin muscles which run to several points on the odontophore, including the base of the large dorsal odontophoral protractor muscles. The ventral odontophoral retractor muscles are not connected to the epiproboscis as they are in *Strigatella*, but a muscular cavity houses the organ below the entire length of the odontophore, whereas in *Strigatella* it is only enclosed below the buccal region. The detailed structure of this organ, however, is very like that of *Strigatella*. The salivary ducts are relatively much wider and less convolute than in *Striga-*

tella and the glands have fewer red=
staining cells than pale cells.

The radula of *I. conularis* (=*I. conica*)
has been figured by Thiele (1929, p 341,
fig. 402) and Cernohorsky (1965, 1966),
and that of *I. conovula*, which has not
previously been illustrated, is here fig-
ured for comparison with that species
(Fig. 1E).

There is no sign of the peculiar
"typhlosole" or of a valve of Leiblein
in the mid-oesophagus, and the glandular
epithelium of that region is more thickly
developed than in *Strigatella*. The sto-
mach and crop are similar to those in
Strigatella, although the crop does not
appear to be ciliated, and the intestinal
region of the stomach has only a few low
ridges developed. The digestive gland,
rectum and anal gland are like those of
Strigatella. The crop and rectum con-
tained radula teeth of what appear to
be turrid and rhipidoglossan gastropods.

The genital systems of *I. conularis*
differed in some respects from those
of *Strigatella*. No information about
these systems was obtained from the
specimen of *I. conovula*. The tightly
coiled seminal vesicle was lined with
an epithelium varying from cuboidal to
squamous, but no indication of sperm
ingestion was seen. A gonopericardial
canal could not be identified in the avail-
able material. The prostate gland, al-
though relatively narrower, had the same
structure as in *Strigatella*. The ejacula-
tory and penial ducts, however, are sur-
rounded by a thick layer of circular
muscle, and also retain the ciliated
epithelium seen in *Strigatella*. The penis
is relatively much longer than in *Striga-
tella*, and has the same structure.

The ovary and ova are like those of
Strigatella. The presence or absence
of a gonopericardial canal could not be
verified. The albumen gland, ingesting
gland and its duct, and the capsule gland
all appeared to be the same as in *Stri-
gatella*, although the ventral channel of
Imbricaria (Fig. 4H) has an additional

short, ciliated fold on the right. In
marked contrast to *Strigatella*, the bursa
copulatrix of *Imbricaria* has a massive,
muscular, internally ridged wall and the
pallial opening is wider. It opens directly
into the bursa and to the vestibule by
way of a short, but very narrow vagina
buried in the bursal wall. The pedal
gland, as far as can be judged from
sectioned material, is relatively larger
than that structure in *Strigatella*.

In summary the anatomy of *Imbricaria*
species differs from that of *Strigatella*
in the relatively longer epiproboscis,
shorter proboscis, small differences in
the buccal musculature and in the lack
of a typhlosole and valve of Leiblein on
the mid-oesophagus. The muscular
sperm duct and the massive, internally
ridged bursa copulatrix are the main
features of the reproductive tracts that
differ from *Strigatella*.

MITRA SPECIES

The proboscides of several species of
Mitra have been examined and these are
of the same general plan as that of
Strigatella paupercula. These species
include: *M. mitra* (Linnaeus), Apia, Sa-
moa (Fig. 9B); *M. stictica* (Link) Nuie;
M. eremitarum Röding, Malekula Is.,
New Hebrides; *M. chrysostoma* Brode-
rip, Port Vila, Éfaté Is., New Hebrides;
M. nigra (Gmelin), Long Reef, New
South Wales. Some variation in the
relative size of the buccal mass and
epiproboscis and in the development of
the peristomal rim was observed (Table
2), but there was remarkable conformity
to the plan found in *Strigatella*. In all
cases, the proboscis was long and, when
retracted, folded into the proboscis sac.
The proboscis of *M. chrysostoma* was
sectioned and found to be of nearly iden-
tical structure to that of *Strigatella*.

The peristomal rim reaches its great-
est development in *M. stictica* where it
overhangs the relatively minute mouth.
Its anterior surface is strongly pleated
and has quite a different appearance
from the outer surface. This rim also
reaches a greater development in the

TABLE 2. Relative dimensions of the shell, buccal mass and epiproboscis
in *Mitra* species.

Species	Length of shell	Length of buccal mass (excluding buccal cavity)	Length of retracted epiproboscis behind buccal cavity
M. mitra	79 mm	2. 3 mm	4. 5 mm
M. stictica	53. 5 mm	4. 5 mm	4 mm
M. eremitarum	48 mm	2. 4 mm	4 mm
M. nigra	55 mm	5. 5 mm	10 mm

Each measurement based on a single specimen.

other species of *Mitra* in comparison with *Strigatella*.

PART 2

AUSTROMITRA RUBIGINOSA (Hutton)

1873 *Columbella* (*Atilia*) *rubiginosum* Hutton, Cat. Mar. Moll. N.Z., p 20.
1913 *Vexillum rubiginosum;* Suter, Man. N.Z. Moll., p 366, pl. 18, fig. 7.
1927 *Austromitra rubiginosa;* Finlay, Trans. N. Z. Inst., 57: 410.
1970 *Austromitra rubiginosa;* Cernohorsky, Bull. Auck. Inst. Mus. 8: 57, pl. 10, figs. 5-10.

Austromitra rubiginosa lives beneath stones in the lower littoral throughout New Zealand. It feeds, as also recorded by Morton & Miller (1968), on various species of tunicate, both solitary and compound, and its egg capsules are found embedded in their tests.

The black shell is usually about 8 mm in length, although it occasionally reaches a height of 10 mm, has a tall spire with weak axial ribs, and a narrow white band just below the periphery. The orange columella has 4 strong plaits, and the aperture has a short anterior canal. This species shows considerable regional variation, particularly in shell colour and in the strength of axial rib-

bing. The material examined was collected at Leigh, north of Auckland, where it occurs with a closely allied species, *A. rubiradix* Finlay.[2]

The living animal has a moderately long, slender siphon which projects well beyond the short anterior canal of the shell aperture. A broad, black band encircles the basal half of the siphon, the rest being white. There are black, radiating patches which are variable in number and pattern on the dorsal surface of the foot, and the rest of the foot is translucent-white with opaque-white spots. Long tentacles with black or grey bases lie on either side of the head which is black or grey dorsally, the rest being white. There is no trace of an operculum. The foot has short lateral projections anteriorly and a slit, the anterior mucous gland aperture, across the front edge. The head-foot of *A. rubiradix* differs from *rubiginosa* in having much more black pigmentation.

The mantle cavity has no unusual features. A large, pale brown osphradium lies on the left alongside the ctenidium which has triangular filaments, their bases slightly narrower than their height. The hypobranchial gland secretes a dense, pale yellow-green secretion, and cells of this colour are scattered amongst opaque-white and colourless cells. All

[2]Cernohorsky (1970: 57) regards *A. rubiradix* as a synonym of *A. rubiginosa*.

cell types occur in approximately equal numbers and have a rather even distribution throughout the gland. The mantle ciliation is normal in pattern, with a particularly strong exhalant current on the right side which carries waste material to the exterior.

The circum-oesophageal ganglia are shown in Fig. 6D (p 319). Concentration is fairly advanced although all of the ganglia except for the pleurals are separate. The supra-oesophageal ganglion has a rather long connective but the sub-oesophageal ganglion is very close to the right and left pleural ganglia. The cerebral ganglia are joined by a very short, broad commissure.

The renal organ resembles that of *Nucella* and *Buccinum* in Perrier's (1889) pycnonéphridiens in having the primary and secondary renal lamellae intermingled.

The Alimentary Canal

The Proboscis. When retracted the short, broad pleurembolic proboscis (Figs. 5A, 9D) has the posterior part of the buccal mass projecting from its inner end. The rather muscular proboscis sheath is attached in front to the cephalic cavity by a ring of retractor muscles and forms the basal part of the proboscis when it is protracted. Although repeated attempts were made to induce the animal to feed in the laboratory, they were not successful, so the total length of the extended proboscis and the feeding mechanism were not observed. It appears, however, that the proboscis is not capable of great elongation.

Cuboidal cells covered with cuticle, and abundant goblet cells make up the outer epithelium of the proboscis and its sheath, apart from the anterior portion of the latter which is ciliated. The proboscis wall consists of a thin outer layer of circular muscle and an inner longitudinal layer. This wall is thinner at the anterior end and there are a few subcutaneous gland cells amongst the underlying connective tissue and longi-

tudinal fibres. When the proboscis is opened the delicate, narrow oral tube (o.t) leading from the minute mouth can be seen. A thin-walled oral invagination has a cuboidal epithelium continuous with that of the outer wall, and this short tube opens into a rather muscular, very narrow part of the oral tube. The minute accessory salivary gland duct opening is on the antero-ventral edge of this muscular part of the oral tube, which is also rather short and is joined to the proboscis wall by a series of thin, radiating retractor muscles (o.t.r). The anterior invaginated portion is connected by only a few thread-like fibres. The muscular part of the oral tube has a ciliated, cuboidal epithelium, but behind this region the cuboidal epithelium is non-ciliated and the oral tube very thin-walled and concertinaed against the buccal cavity. This part of the tube lies loose in the proboscis cavity, but the buccal cavity is firmly fixed to the proboscis wall by numerous, thin, short, buccal tensor muscles. The buccal walls are very muscular, and are lined with cuticle ventrally, whereas those above remain ciliated. Presumably the odontophore traverses the entire oral tube, but it is not clear how this is achieved.

The salivary ducts migrate down the sides of the small buccal cavity to open latero-ventrally near its anterior end. The moderately large odontophore (od) protrudes into the buccal cavity. Well-developed muscles surround the large cartilages and a rather slender odontophoral retractor muscle (Fig. 9, p 331 od.r) runs from the posterior end of the odontophore to the floor of the cephalic cavity. Although functionally a single muscle, it consists of partially fused right and left elements. The rather broad radular sac is the same length as the odontophore and the teeth are very like those of the genus *Vexillum*. These consist of 2, curved, simple, lateral teeth and a broad central tooth in each row. The central is slightly arched and has 15 pointed cusps (Fig.

5B). *A. rubiradix* has the same number
of cusps on the central, but the lateral
teeth bear very minute denticles (Fig.
5E). There is no epiproboscis.

The Oesophagus and Salivary Glands.
The first portion of the anterior oeso-
phagus has muscular walls consisting
of an inner longitudinal and an outer
circular layer, but the posterior part
has very thin walls. Short, ciliated
cuboidal cells cover the prominent dor-
sal folds of the anterior oesophagus,
while the non-ciliated ventral channel and
the longitudinally ridged dorsal food
groove are lined with cuboidal epithe-
lium. Only a few goblet cells can be
found in the anterior oesophagus, this
being in marked contrast to the situation
found in *Strigatella*.

The wide salivary ducts are about
50 μ in diameter and lie buried in the
dorsal folds which they enter just in
front of the valve of Leiblein. They
are lined with ciliated cuboidal cells,
and the short, free sections of the ducts
are surrounded by a few circular mus-
cle fibres. The ducts enter the large
glands (s.g) near their antero-median
edges. They lie mostly on the left and
in the middle of the cephalic cavity and
cover most of the anterior, and some of
the mid-oesophagus. Each gland con-
sists of close-packed, semi-discrete
tubules which are made up of cells
containing masses of purple-red-stain-
ing granules.

The accessory salivary glands (a.s.g)
are large vesicles up to 250 μ in dia-
meter which are lined with a non-ciliated
pavement epithelium, and outside this,
a coat of inner longitudinal muscles and
outer circular muscles. Each vesicle
is filled with a pale-blue-staining se-
cretion derived from a mass of gland
cells lying outside the muscle layers.
These cells are in 2-3 layers and stain
bluish-purple. The structure of these
glands is thus very like the accessory
salivary glands of *Alcithoe* (Ponder,
1970) and many other rachiglossans.
The ducts of the accessory salivary
glands (a.s.d) are lined with a non-

ciliated, cuboidal epithelium and are
surrounded initially by a few circular
muscle fibres, outside of which is a
single layer of gland cells. As the
ducts approach the proboscis they lose
the glandular tissue, become narrower
and eventually join below the odonto-
phore to form a single, very narrow,
coiled duct.

The valve of Leiblein (v.l) is a rela-
tively large bulb about 260 μ in diameter.
Its thick glandular walls consist of 2
different-staining regions as is normal
in this structure (Graham, 1941; Wu,
1965). The anterior portion consists of
tall, colourless to pale blue-staining
cells which bear very long cilia, whereas
the posterior portion has taller cells
that stain dark purplish-red to purplish-
blue and have short cilia. Very long
cilia, which arise from a ring of colum-
nar cells at the posterior rim of the
anterior oesophagus, mingle with those
of the first glandular region to form a
cone-like mass in the middle of the
valve, but there is no projecting rim
derived from the anterior oesophagus as
there is in the muricids (Graham, 1941;
Wu, 1965) and in *Alcithoe* (Ponder,
1970). The ventral groove of the ante-
rior oesophagus remains as a ventral,
non-ciliated slit throughout the valve of
Leiblein. Just behind the valve the mid-
oesophagus suddenly narrows and passes
through the nerve ring and its walls
become thin with weak longitudinal rid-
ges. The ventral groove is represented
by a narrow, non-ciliated ventral strip
with low dorsal folds lying on either
side. The remainder of the epithelium
is ciliated and has abundant goblet cells,
but as the mid-oesophagus nears the
posterior side of the nerve ring these
become less common. Behind the nerve
ring the mid-oesophagus suddenly ex-
pands, its walls becoming thick and
glandular. This epithelium is made up
of tall gland cells containing irregular
granules that appear semitranslucent
white in life, but stain purplish-red,
and these alternate with short, wedge-
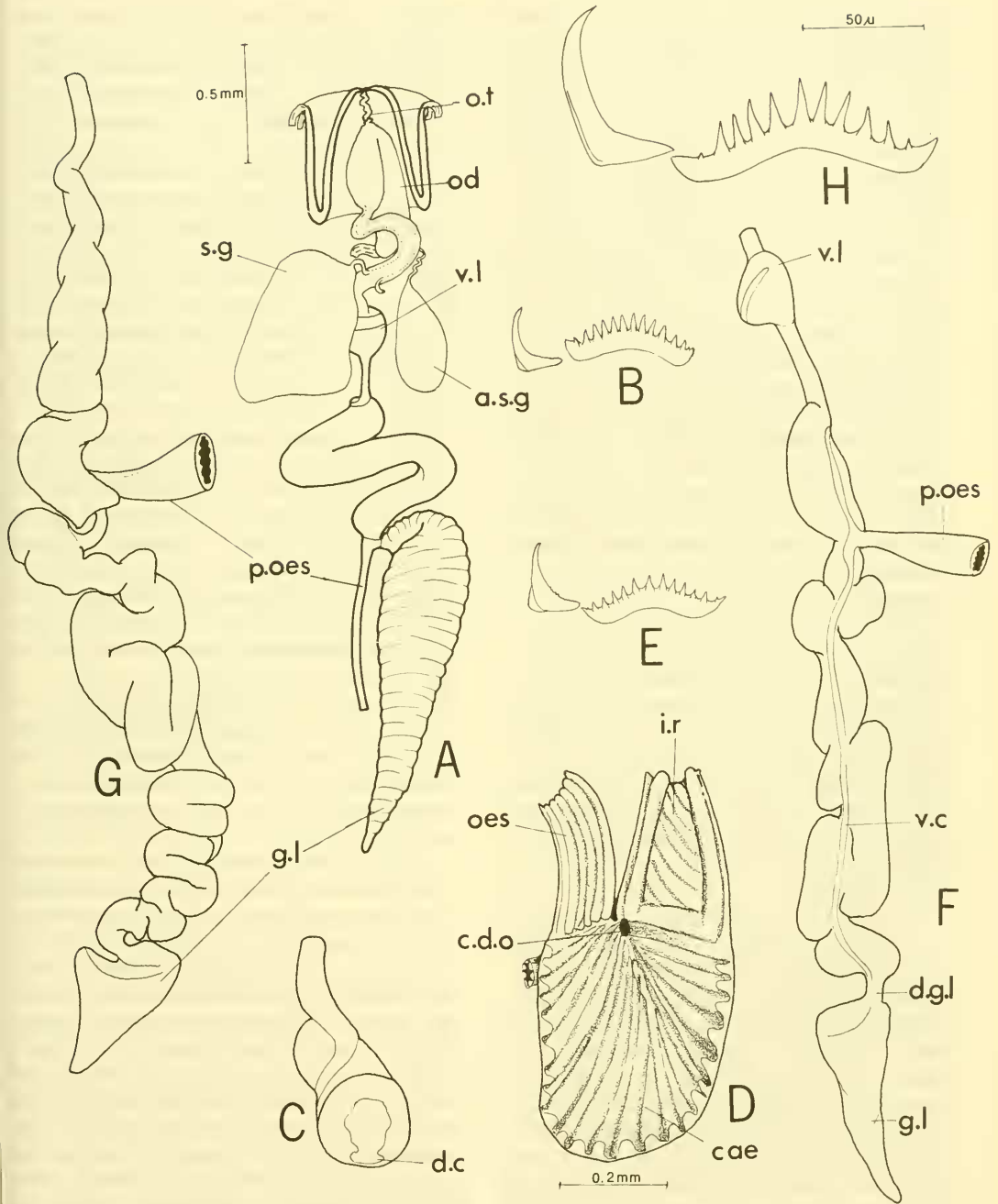shaped ciliated cells. Torsion occurs

FIG. 5. A–D. *Austromitra rubiginosa* (Hutton): A. Anterior alimentary canal; B. Radular teeth (Leigh, north of Auckland); C. The portion of the mid-oesophagus just behind the nerve ring showing torsion; D. The stomach opened dorsally. E. *Austromitra rubiradix* Finlay. Radular teeth (Leigh, north of Auckland). F. *Vexillum luculentum* (Reeve). Mid-oesophagus ventral view. G–H. *Vexillum plicarium* (Linnaeus): G. Mid-oesophagus, dorsal view; H. Radular teeth (Port Vila, Éfaté Island, New Hebrides).

just behind the commencement of the glandular region (Fig. 5C) so that the now weakly ciliated, thin-walled, dorsal food channel (d.c) lies ventrally. The ventral groove is completely obliterated by the glandular epithelium covering the entire pretorsional ventral and lateral walls. The pretorsional upper edges of the dorsal folds persist as columnar ciliated cells throughout the remainder of the mid-oesophagus, this being rather long and folded up in the cephalic cavity behind the salivary glands and in front of the gland of Leiblein.

The very short duct of the gland of Leiblein opens on the right ventral side of the mid-oesophagus at the end of the glandular region. This position is unusual in the Neogastropoda, since in most other species the duct opens dorsally. The duct has the 2 pretorsional ventral oesophageal folds lying on its posterior surface, and these run obliquely into the dorsal side of the posterior oesophagus where they disappear. The duct is lined with a continuation of the epithelium making up the gland of Leiblein and the ventral folds, the latter nearly entering the gland before they terminate. The unusual orientation of this duct suggests that it has been forced ventrally by the glandular development of the mid-oesophagus following the occlusion of the ventral groove.

The gland of Leiblein (g.l) lies on the right side of the posterior oesophagus and is an elongate, pyriform body, dark greenish-brown in life, transversely wrinkled, with the anterior end, from which the duct leaves, bent back on itself on the left side of the gland. Its lumen is subdivided into semi-tubular compartments by thin, muscular partitions. The whole of the gland is lined with tall gland cells which nearly fill the lumen and it is surrounded by a thin, muscular coat. The gland cells have basal nuclei and many bear short cilia. They appear to undergo a secretory cycle commencing with short cells with orange-red to brownish-staining granules in a purplish-blue-staining cy-

toplasm. As the cells enlarge the granules increase in quantity, and when almost at full size green-staining granules appear. These accumulate with the other granules at the distal ends of the cells and at this stage the cilia appear to be lost. A vacuole then generally appears below the distal granular mass which is budded off while the red granules re-accumulate in the basal part of the cell and the cycle recommences. The distal end of the gland is a single tubule, the epithelium of which is not actively glandular but otherwise resembles that of the rest of the gland.

The posterior oesophagus (p.oes) is a narrow, thin-walled tube with no distinct crop region. It is surrounded by a few muscle fibres and there are about 6 longitudinal ciliated ridges. There are a few large goblet cells, but otherwise it is non-glandular. The spherules from the gland of Leiblein and the granular secretion from the mid-oesophagus can be observed in its lumen.

The Stomach and Digestive Gland. The rather small, U-shaped stomach (Fig. 5D) has a very delicate outer wall. The oesophagus (oes) opens into the stomach on the left side and the intestine emerges alongside on the right. Posteriorly there is a short caecum (cae) which has numerous radiating folds on its walls. The intestinal half of the stomach is occupied largely by a style sac (i.r). This has 2 dorsal typhlosoles and a low transverse ridge which marks its posterior limit. Alongside the posterior edge of this ridge a groove leads to the single digestive gland aperture (c.d.o) which lies in the middle of the stomach at the bend in the U. Thus it lies in close proximity to both the style sac and the opening to the oesophagus. The ciliated gastric epithelium consists mainly of columnar cells, and there are no cuticle-lined surfaces.

The digestive gland duct divides into 2 just below the stomach, the dorsal branch passing to the small anterior lobe of the gland which lies above the

intestinal part of the stomach, and the other branch running to the massive posterior lobe. The epithelium of the digestive gland is like that of *Strigatella*, but there were none of the amoebocytes, which characteristically store greenish granules, present in the digestive glands of the 4 specimens sectioned.

The Intestine and Anal Gland. The intestine runs from the stomach through the renal organ and along the right pallial wall. It is lined with columnar cells bearing long cilia. Numerous yellow to orange-staining gland cells occur in the rectum.

The anal gland (Fig. 6C; a.g) is represented by only a single tubule which lies above the rectum and opens into it at the level of the anal aperture. Its cells are cuboidal or short-columnar and non-ciliated, with large spherical nuclei and dense yellowish-brown granules in the cytoplasm. Unlike the usual type of anal gland epithelium they do not appear to bud off their apices.

The Male Genital System

The Testis and Vas Deferens. The testis lies on the ventral surface of the visceral mass where its tubules form a compact mass and do not ramify through the digestive gland. The vas deferens is swollen into a coiled seminal vesicle which is lined with pavement epithelium and does not appear to ingest sperm. It is confluent with a moderately wide, ciliated duct, the renal vas deferens, which is longitudinally ridged and opens into the prostate gland at the posterior end of the pallial cavity. There is no gonopericardial canal.

The Prostate Gland. The initial portion of the large prostate gland (Fig. 6A; pr) has an enclosed, non-ciliated lumen with the renal vas deferens buried in its inner wall. At the point where this opens, the lumen of the prostate gland becomes ciliated and a short fissure is formed ventrally. The greater part of the prostate is, however, an enclosed tube, circular or oval in section and about 0.34 mm in diameter with a very narrow, ciliated lumen. There is no trace of a line of fusion such as that seen in *Ocenebra* (Fretter, 1941). The prostatic cells which contain purple-red-staining granules, are arranged in an irregular mass around an inner epithelial layer. This inner layer is similar in staining properties to the rest of the prostatic cells, but its cells are columnar in shape and alternate with ciliated cells.

The prostate becomes narrower in the anterior part of the pallial cavity where it passes on to the floor of the cephalic sinus as the ejaculatory duct. This duct is not muscular and is surrounded by a glandular epithelium which stains blue near the base of the penis.

The Penis. The massive penis (pen) lies on the right side of the body at the base of the pallial cavity. It is oval in section and tapers to a blunt point at which the duct opens. The outer surface is covered with a thick layer of cuticle which is secreted by a cuboidal epithelium. Immediately below this epithelium is a thin layer of circular muscle which surrounds the bulk of the penial tissue. This consists of an interwoven mass of variously orientated muscle fibres amongst which are minute blood spaces and connective tissue. The ciliated penial duct has a fairly wide lumen and is central in position.

The Female Genital System

The Ovary. The ovary contains large ova up to about 300 μ in diameter which have large yolk granules. The ovarian tubules remain separate from the digestive gland. The upper oviduct is short and straight, and has an irregular, non-ciliated columnar epithelium. The rather short renal oviduct is lined with tall ciliated cells and, although it crosses the pericardial wall, there is no gonopericardial duct.

The Albumen Gland. The posterior end of the albumen gland (Fig. 6B; alb) bulges into the anterior wall of the renal organ and has a simple glandular epithelium up to 140 μ thick consisting of

a single layer of cells. The renal oviduct opens near the anterior end of the albumen gland and, at this point, the glandular epithelium changes from purplish-blue to very pale pink-staining cells. These give way ventrally to a groove lined with a cuboidal epithelium. This groove is continuous with the ventral channel of the capsule gland. The pale pink-staining lateral walls are continuous between the capsule gland and the albumen gland, though there is a change to a bright red-staining region at the commencement of the capsule gland.

The Ingesting Gland. The ingesting gland duct opens into the ventral channel between the junction of the albumen and capsule glands on their outer side. It is like that of *Strigatella*, but has 1 or 2 very prominent longitudinal folds in the upper half. As in *Strigatella* it opens into the ingesting gland dorsally. This gland (i.g) is also like that of *Strigatella*, being a simple pouch lined with tall cells with large spherical, basal nuclei. Groups of orientated spermatozoa from the bursal duct lie in the lumen of the gland amongst masses of unorientated sperm which are ingested by the epithelial cells. These cells contain bluish-purple-staining vacuolate cytoplasm, but have no yellow granules like those typically seen in many rachiglossans.

The Capsule Gland. The capsule gland (cap) closely resembles that of *Strigatella* and shows similar zones in the posterior part. Owing to the smaller size of this species, however, the epithelium is nearly all of the simple glandular type, only the mid-lateral walls of the middle region of the capsule gland having a complex glandular epithelium such as that seen in most larger rachiglossan species. The middle region of the gland differs slightly from that of *Strigatella* as there is an orange-red-staining zone in the lower half separated by a narrow wedge of blue cells from a dorsal, pale pink-staining area.

The ventral channel is lined with a ciliated epithelium and differs from that of *Strigatella* in having a bilobed left, and a single right ciliated fold overhanging it. In addition, through most of its length there is a low ciliated ridge along its centre.

The Vestibule, Vagina and Bursa Copulatrix. The anterior region of the oviduct is also like that of *Strigatella* in general plan. An anterior, vertical strip of pale pink-staining glandular epithelium up to 120 μ in thickness, gives way suddenly to a thin-walled vestibule with narrow, longitudinal ridges and is lined with short columnar and cuboidal cells which have only a few mucous cells amongst them. The vestibule rapidly narrows until it is only a narrow, ventrally placed tube (va). This has a thin muscle coat and is lined with columnar cells laterally and dorsally, but cuboidal cells ventrally. These latter cells are continuous with the ventral channel of the capsule gland. This tube, the vagina, lies below and on the outside of a long muscular bulb, the bursa copulatrix (b.c). Both the vagina and the bursa copulatrix open at the large pallial opening or gonopore, which is located just behind the anterior extremity of the bursa. The walls of the gonopore are heavily folded and lined with ciliated columnar cells. Behind the gonopore the cells are covered with cuticle. Masses of spermatozoa lie with their heads embedded in the bursal walls, but are also found free in the bursal lumen and attached to the walls of the anterior part of the vagina. There was no indication of a ventral pedal gland in either of the 2 mature females sectioned.

The Egg Capsules. Egg capsules (Fig. 6E) are found throughout most of the year embedded in the tests of various species of compound and colonial tunicates. They are transparent, horny and hemispherical, with the flat side outermost. Usually 3-5 eggs are included in each capsule and as many embryos develop, so that no cannibalism appears to occur. The juveniles escape by making an irregular rent in the outer surface of the capsule. They are white and have no operculum. The shells consist of the pink protoconch of 2 whorls, and at this stage they have 3 columellar plicae.
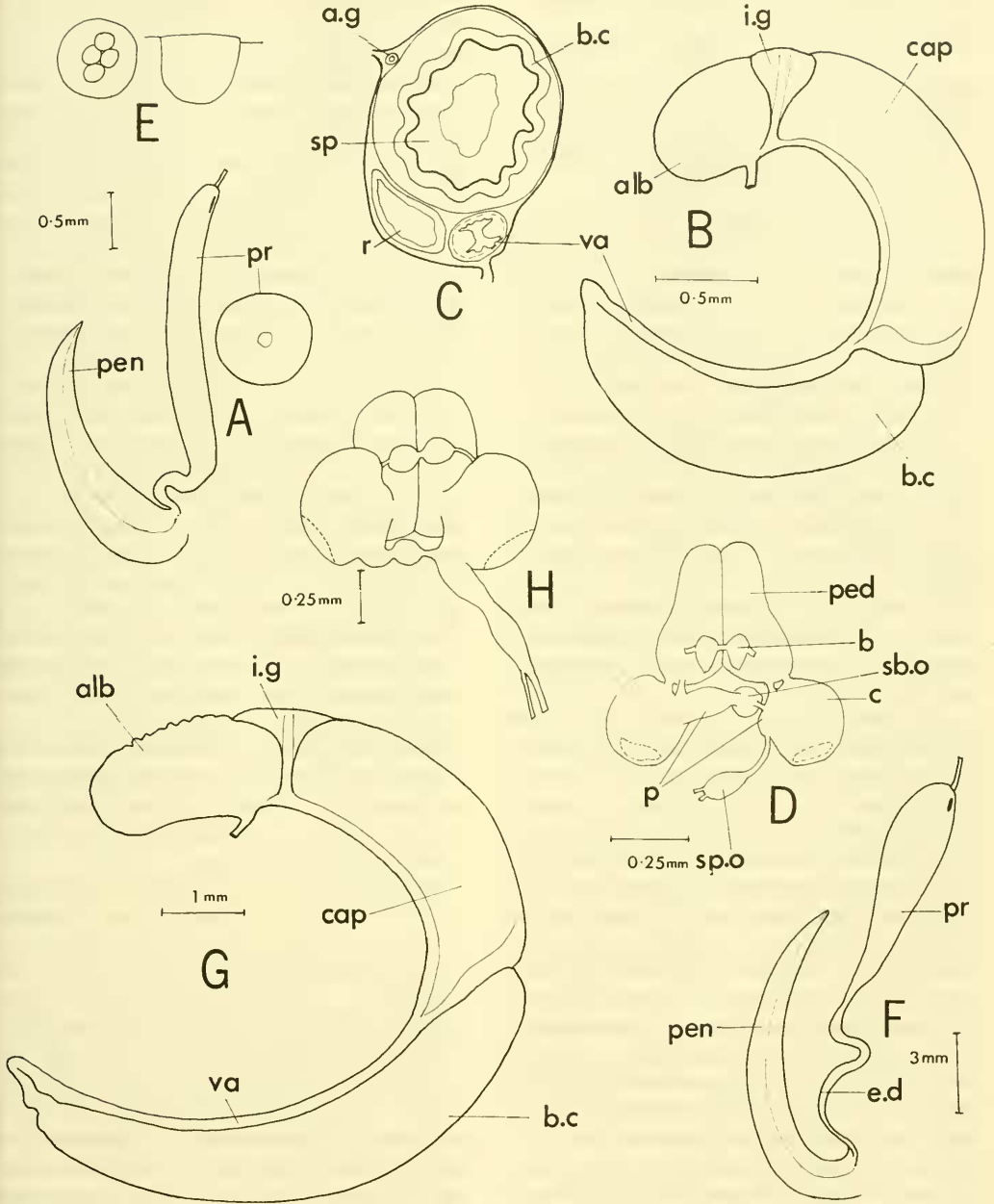
FIG. 6. A–E. *Austromitra rubiginosa* (Hutton): A. A diagram of the pallial part of the male genital system, including a transverse section of the prostate; B. A diagram of the pallial oviduct seen from the right; C. A transverse section of the bursa copulatrix and vagina; D. A diagram of the circum-oesophageal ganglia viewed dorsally with the cerebral ganglia separated and spread apart; E. Dorsal and lateral view of egg capsule. F. *Vexillum plicarium* (Linnaeus). A diagram of the pallial part of the male genital system. G. *Vexillum luculentum* (Reeve). A diagram of the right side of the pallial oviduct. H. *Strigatella paupercula* (Linnaeus). A diagram of the circum-oesophageal ganglia viewed dorsally with the cerebral ganglia separated and spread apart (for explanation see fig. D).

VEXILLUM LUCULENTUM (Reeve)

1845 *Mitra luculenta* Reeve; Conch. Icon.
    pl. 30 sp. 245.
1965 *Pusia luculenta*; Cernohorsky, Ve-
    liger, 8: 147, pl. 22, fig. 122.
1966 *Vexillum luculentum*; Cernohorsky,
    Veliger, 9: 120, text fig. 41.

Cernohorsky (1965, 1966) has de-
scribed the external colouration of the
animal, the shell, habitat preferences
and radula of this species. Risbec
(1928) also described the shell, radula
and external features of *V. luculentum*
as well as the gross anatomy of the
alimentary canal and pallial cavity.

The material described here was col-
lected in the middle intertidal zone at
Port Vila, Éfaté Island, New Hebrides.

This species is small for the genus,
being 8-15 mm in height (Cernohorsky,
1965). A few differences in the alimen-
tary canal and genital systems exist
between *V. luculentum* and *Austromitra*
rubiginosa and these are summarised
below.

The retracted proboscis is a little
longer than that of *Austromitra* but the
buccal mass still projects into the ce-
phalic cavity. A very narrow, short
oral invagination recalls that of *Austro-*
mitra in structure, but the muscular part
of the oral tube behind it is not ciliated,
although it is lined with cuboidal cells.
The posterior part of the oral tube is
even more muscular than the middle
portion and is ciliated, both of these
features being in contrast to the situation
in *Austromitra*. The posterior part of
the oral tube, as in *Austromitra*, is not
attached in any way, and the middle
part is fixed to the proboscis wall by
slender retractor muscles.

The mid-oesophagus (Fig. 5F) shows
the greatest differentiation from *Austro-*
mitra of any structure in the alimentary
canal. The long glandular part has
become mostly separated from the con-
ducting tube and forms a long, convolute
structure that is attached to the short,
triangular gland of Leiblein. The de-
tached portion of the mid-oesophagus is

surrounded by a thin layer of muscle
and the growth of its glandular walls
has apparently outpaced that of a narrow
thin-walled ventral channel (v.c) which
runs between them. This channel is lined
with a very thin, non-ciliated epithelium
which contains minute greenish granules
similar to those in the cells of the gland
of Leiblein. The original duct of this
gland (d.g.l) is still apparent as a nar-
row portion between the mid-oesophageal
section and the true gland of Leiblein,
but all traces of the pretorsional ventral
folds have been lost. The gland of
Leiblein has a thick, muscular wall
with an outer longitudinal and inner
circular layer. The glandular epithe-
lium is not as well developed as it is
in *Austromitra* and secretory activity
is much less pronounced. The torsional
area and general cytology are otherwise
like the those of *Austromitra*. Although
the posterior oesophagus (p.oes) has a
somewhat greater diameter than that of
Austromitra no crop-like structure is
developed. The remainder of the ali-
mentary canal is very like that of *Aus-*
tromitra except that the 2 digestive gland
ducts open into the stomach separately,
although these are close together in the
same area as the opening of the single
duct in *Austromitra*.

The male genital system is very like
that of *Austromitra* but the female differs
in some respects. Because of the some-
what larger size of this species the
glandular epithelium of the albumen
gland and capsule gland is arranged in
complex, multicellular units, except for
the dorsal glandular strip of the capsule
gland. The capsule gland (Fig. 6G; cap)
is short in relation to the length of the
bursa copulatrix, but is similar to that
of *Austromitra* except that the ventral
channel has a short right ciliated fold
and 2 left folds. The lower left fold is
about the same size as that on the right,
but the upper one is considerably longer.
The very long vagina (va) is divided
into upper and lower halves by a long
left fold and short right folds and opens,
together with the bursal duct, at a small,

muscular gonopore.

The bursa copulatrix (b.c) is much longer than that of *Austromitra* and it differs in several other respects. Only unorientated sperms are stored there and its thinly muscular wall is not internally ridged. It is lined with tall columnar cells, about 50 μ in height, containing red-staining globules which are secreted, along with blue-staining granules, into the bursal lumen and appear in considerable quantities amongst the masses of spermatozoa. This secretion is possibly responsible for sperm breakdown as intact spermatozoa could only be seen in the proximal end of the bursa, whereas irregular masses of sperm that had undergone changes in appearance and staining properties were found distally. Thus the bursa may supplement the function of the ingesting gland, that is to rid the gonoduct of excess sperm. Glandular bursal epithelia have also been recorded in *Ocenebra erinacea* (Linnaeus) (Fretter, 1941) and in *Oliva sayana* Ravenel (Marcus & Marcus, 1959). The bursal duct is a moderately long, rather twisted, very muscular canal lined with a ciliated epithelium. There was no sign of a ventral pedal gland.

The renal organ of this, and the following species, is like that of *Austromitra*.

VEXILLUM PLICARIUM (Linnaeus)

1758 *Voluta plicaria* Linnaeus; Syst. Nat. ed. 10, p 732, no. 366.
1965 *Vexillum plicarium*; Cernohorsky, Veliger, 8: 132, pl. 20, fig. 94.

The shell of this handsome species has been described and figured by Cernohorsky (1965) and the radula by Troschel (1856, pl. 9, fig. 15). The material described here was collected at Port Vila, Éfaté Is., New Hebrides.

The adult shell is 34-50 mm in height (Cernohorsky, 1965) and is thus much larger than both of the foregoing species. The head-foot is like that of other species of the genus, but details of the

considerable external pigmentation could not be determined adequately in the preserved material.

The mantle cavity has a relatively smaller osphradium and a larger gill than either of the other 2 much smaller species, the osphradium being about $^2/_3$ of the length of the gill, and about $^1/_2$ its width. Differences in the proportions of pallial structures are, however, usual in allied species that show a considerable discrepancy in size.

The retracted proboscis of this species is relatively much longer than that of *V. luculentum*. It lies in a muscular sheath on the right side of the cephalic cavity and is then bent to the left. It thus displaces the large salivary glands to the left so that the right gland overlies the left, whereas in *Strigatella* the reverse situation is found. The long, muscular anterior oesophagus runs along most of the proboscis sheath, but at the edge of the salivary glands it descends beneath them. Four powerful retractor muscles lie below the sheath, continuous with the rather thick longitudinal muscles in its wall. The slender proboscis lies with its pointed distal end sometimes protruding into the snout. The structure of the proboscis (Fig. 9E) is similar to that of the 2 preceding species and is particularly like that of *V. luculentum*. The outer epithelium, however, is columnar and most of the oral tube is lined with columnar cells. Unlike that of *V. luculentum*, the oral invagination, which is exceedingly narrow, is ciliated, but the next portion, to which the retractor muscles are attached, has a non-ciliated cuboidal epithelium. The posterior part of this tube is relatively wider and much folded, and has a ciliated columnar epithelium. The very narrow, common duct of the accessory salivary gland opens on the anterior extremity of this latter region.

The mid-oesophagus (Fig. 5G) closely resembles that of *V. luculentum*, although the gland of Leiblein (g.l) is shorter than in that species, being about as broad as it is long and having a

thicker muscular coat with variously orientated fibres. In addition the glandular lining is much reduced and delicate, although the cells are of the same type as in *Austromitra* and occasional budding of their distal ends occurs. The lumen of the gland is not subdivided, is relatively wide and contains granules of secretion from the separated mid-oesophageal region attached to the gland. The gland of Leiblein presumably acts as a pump in the same manner as the poison bulb in the Toxoglossa.

The posterior oesophagus (p.oes) is much wider than that of either of the other 2 species in this group. Its walls have very high lamellae which develop secondary and, posteriorly, tertiary folds, which consequently occupy much of the lumen. The function of these lamellae is possibly absorptive as they are rather vascular, especially posteriorly.

The stomach is relatively smaller than that of *V. luculentum* and *Austromitra*, and has 2 digestive gland openings. The narrow intestine resembles that of the other 2 species and the anal gland is also similar, although the single tubule develops short side-branches.

The male genital system follows the same plan as that of *Austromitra* but the prostate (Fig. 6F; pr.) is relatively shorter, and the posterior opening appears to be restricted to a small pore. The penis (pen.) is long and slowly tapering and its duct is centrally placed as in the other 2 species. Unfortunately, no male specimen was available for histological examination.

The female genital structures were examined histologically in 1 specimen and, although there was no female available for dissection, the general plan of the genital tract appears to be like that of *V. luculentum*. The mature ovary is massive, sharply differentiated from the digestive gland and contains ova up to 240 μ in diameter. There is no gonopericardial duct and the renal oviduct is embedded in the pericardial wall as in the 2 allied species and

Strigatella. The larger size of this species has resulted in a much greater development of the lateral walls of the albumen and capsule glands than was observed in the smaller, preceding species. Larger size has also resulted in the subdivision of the ingesting gland into several compartments, and its relatively narrow duct is surrounded by a massive layer of circular muscle. In other features, however, this gland has the same structure as that of *Austromitra* and *V. luculentum*. The ventral channel of the capsule gland has a long left fold, with 2 low ridges on its under surface, and a low median fold lying immediately below the innermost secondary ridge of the left fold. Thus a sperm channel on the left is separated from an ovarian channel on the right. The vagina also shows a division into 2 separate channels as in *V. luculentum*, but the folds on either side are of equal length. The bursa copulatrix does not appear to be as long as it is in *V. luculentum*, but it is lined with the same epithelium as seen in that species, the cells being about 50 μ high. The bursal walls, however, have low, longitudinal folds, and the muscular bursal duct is like that of *V. luculentum*. No orientated spermatozoa were observed in the bursa.

The differences in the mid-oesophagus and bursa copulatrix suggest that generic separation is justified for *Austromitra*, despite its radula being similar to *Vexillum* species. The simple structure of the mid-oesophagus, including the primitive nature of the gland of Leiblein in *Austromitra*, suggest that it is less advanced than *Vexillum* species in terms of evolutionary development.

PART 3

PECULATOR HEDLEYI (Murdoch)

1905 *Velpecula* (*Pusia*) *hedleyi* Murdoch; Trans. N.Z. Inst., 37: 228, pl. 8, fig. 21.
1937 *Peculator hedleyi*; Powell, Discovery Rept. 15: 212.

The shell of *P. hedleyi* is adequately de-

scribed and figured by Cernohorsky (1970: 116, pl. 14, figs. 15-16) but no information on the soft parts has been published.

Living specimens of *P. hedleyi* were obtained in shell sand from just below extreme low water to about 2 fathoms deep in Taurikura Bay, Whangarei Heads and in 6-18 fathoms in the entrance to Port Fitzroy, Great Barrier Island. It is not a common species and appears to be restricted to the north eastern coast of the North Island of New Zealand.

The shell (Fig. 7G) reaches 6.2 mm in height, is inflated, with a short spire which is only $^1/_2$ the height of the aperture. The only sculpture is fine axial growth lines and weak spiral grooves. The disproportionately large protoconch of 2 whorls is uniform brown, but the remainder of the shell has the brown colour broken up by irregular spiral rows of white spots. The long aperture has 4 columellar plaits.

The living animal (Fig. 7G) is translucent white and studded with minute, opaque white spots. Along the lateral parts of the foot there is a pair of opaque white strips which are sometimes broken up into a series of patches. A short siphon projects a little beyond the shell and the rather short tentacles have rounded ends, with the eyes bulging from their outer bases. A minute opercular rudiment lies on the dorsal surface of the posterior end of the broad foot which has a wide, straight anterior end with short lateral projections. The strongly ciliated sole is richly supplied with mucous secretion.

The pallial cavity presents few differences from the species discussed previously. The broad, yellowish-brown osphradium has about 16 filaments which are longer on the right side, and the ctenidium has triangular gill filaments which have bases a little narrower than their height. The hypobranchial gland covers the pallial roof, gonoduct and rectum and has 4 types of cells, all of which are distinguishable in life. Transparent cells occur abundantly throughout the gland while black cells and translu-

cent "crystalline" cells lie over the rectum and gonoduct and are replaced by brown cells throughout the rest of the gland. There is no purple hypobranchial secretion.

The pale greenish renal organ opens posteriorly into the pallial cavity and the mid-oesophagus bulges into the lumen of the cavity from below the thin floor. The single tubule of the anal gland can be seen externally, lying on the right side of the anterior half of the pallial roof.

The circum-oesophageal ganglia (Fig. 8G) are similar in arrangement to those of the foregoing species, although the supra- (sp.o) and sub-oesophageal (sb.o) ganglia are connected to the pleural ganglia (p.) by moderately long connectives. The buccal ganglia (b.) are somewhat displaced to the left. The renal organ is like that of *Austromitra* in having the 2 types of renal lamellae interdigitated.

The Alimentary Canal

The Proboscis. The extended pleurembolic proboscis is moderately long and is of the same colour as the external parts of the animal. It is short when retracted (Figs. 7A, 9G) and the basal portion forms a proboscis sheath. The distal part does not lie entirely within the sheath, but extends forward into a short, ciliated, anterior proboscis cavity which represents an expansion of the rhynchostome (Fig. 9G). The outer epithelium of the proboscis is non-glandular and ciliated, but the sheath is devoid of cilia. The proboscis wall is rather thin anteriorly and consists of a very narrow zone of circular muscles and, inside these, a few longitudinal fibres, the latter being much more prominent in the wall of the sheath. Longitudinal fibres and connective tissue occupy the proboscis cavity and some irregular clusters of red- and blue-staining gland cells lying in this cavity send their ducts to the outer surface of the proboscis.

The buccal cavity has thick, muscular

walls and lies above the narrow odonto-
phore which extends nearly to the tip of
the proboscis in the resting position. A
thick cuticular plate lies below the ante-
rior end of the odontophore just under
the small mouth.   There is no other
appreciable cuticular thickening although
the buccal walls are covered with a thin
chitinous layer.   Weakly ciliated but
prominent dorsal folds lie laterally in
the buccal cavity and have the salivary
ducts embedded in them.   These ducts
pass laterally and then ventrally to dis-
charge near the anterior end of the
odontophore.   A very short, unpaired
accessory salivary gland (a.s.g) dis-
charges below the anterior end of the
odontophore by way of a short, narrow,
muscular duct. This gland is surrounded
by a thin layer of circular muscle and
has an irregular glandular epithelium
which stains pale blue.   There are no
gland cells lying outside the muscle,
contrary to the usual condition in the
accessory salivary glands of other neo-
gastropods.

The odontophoral cartilages (od.c)
are rather small and extend to the inner
end of the retracted proboscis. They
are attached to a mass of muscle which
extends well beyond the inner end of the
retracted proboscis, and thus behind the
odontophoral cartilages. This muscular
rod is circular in section (Fig. 7C) and
is made up of a thick coat of circular
muscle about 50 μ in thickness. It con-
tains a core of longitudinal muscle in
which is buried, for about $1/2$ of its
length, the radular sac (r.s). Behind
the end of the radular sac the muscular
core continues to the end of the muscular
rod to which a short odontophoral re-
tractor muscle (od.r) is attached. There
is no epiproboscis.

Each radular row (Fig. 7D) consists
of a large central tooth, and a pair of
smaller, needle-like lateral teeth. Each
central tooth has a long median cusp
with a transversely concave anterior
surface.   This suggests that each tooth
acts, in part, as a spoon rather than as
a simple cutting tool. The base of each
tooth has a pair of anteriorly bent, long,

narrow plates, the lower portions of
which are curved laterally.

The Oesophagus and Salivary Glands. A
thick wall of circular muscle surrounds
the anterior oesophagus (Fig. 7Ba). Its
non-glandular epithelium is only weakly
ciliated within the dorsal food groove, but
the dorsal folds have moderately strong
cilia.   The salivary ducts lie embedded
in the dorsal folds throughout the ante-
rior oesophagus and enter it just in
front of the valve of Leiblein. They are
ciliated and lined with a squamous epi-
thelium and, where free from the oeso-
phagus, they have a thin outer coat of
muscle.   The small salivary glands
(s.g) lie below the anterior part of the
mid-oesophagus. They are lobed bodies
which are composed of a few semi-
discrete tubules made up of reddish-
staining cells similar to those found in
most neogastropods.   These tubules do
not have any outer muscles and do not
appear to contain any ciliated cells.

The mid-oesophagus (Fig. 7A) is the
most conspicuous part of the alimentary
canal as it forms a long, convolute,
swollen tube lying within the cephalic
cavity. It commences well in front of
the nerve ring as the valve of Leiblein
(v.l), which is slightly wider than the
rest of the mid-oesophagus.   A non-
ciliated channel (v.c), continuous with
the ventral channel in the anterior oeso-
phagus, lies ventrally and a zone of
radial muscles (r.m) on either side
extend from it into the now reduced
dorsal folds.   These muscles persist
right through the valve.   Above the
folds lies the glandular pad usually
found in this structure (Fig. 7Bb). The
most anterior glandular epithelium
stains red (r.c) but a dorsal zone of
mucous cells (m.c) a little behind rapidly
spreads to surround the dorsal glandu-
lar area (Fig. 7Bc). Cells bearing
very long cilia between the mucous
cells and these cilia extend backwards
into the lumen of the gland but there is
no cone-like valve such as is normally
found in this region.   The dorsal folds
remain as a distinct, though reduced,
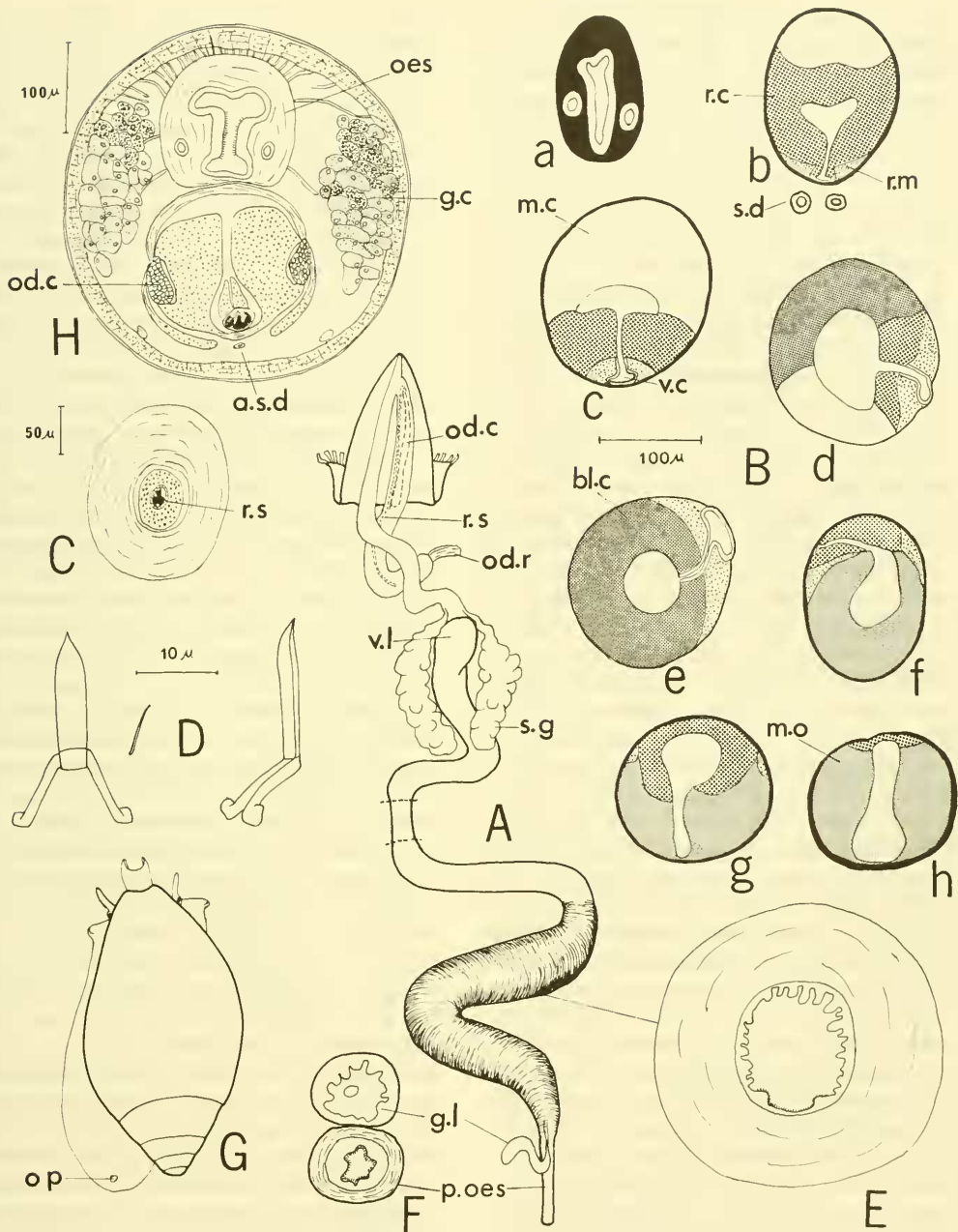region throughout the "valve".   Their

FIG. 7. A–G. *Peculator hedleyi* (Murdoch): A. The anterior alimentary canal showing the proboscis opened. The muscular portion of the mid-oesophagus is cross-hatched; B. (a–h) Transverse sections of oesophagus near and through the valve of Leiblein (for explanation see text); C. A transverse section of the muscular posterior extension of the odontophore; D. Radular teeth, face and lateral view; E. A transverse section of the muscular part of the oesophagus with position of section indicated on fig. A; F. A transverse section of the gland of Leiblein and the posterior oesophagus; G. A dorsal view of the living animal and the shell showing the reduced operculum. H. *Microvoluta marginata* (Hutton). A transverse section of the proboscis.

lower surfaces are lined with a squamous epithelium which covers the muscles referred to above. Their upper surfaces consist of the red-staining gland cells which have persisted from the anterior zone and these reach a maximum height of 40 μ. The supporting cells between these gland cells have only short cilia. About $^2/_3$ of the way through the valve the red cells on the dorsal folds, and the mucous lining in the dorsal groove, are suddenly replaced by blue-staining gland cells (Fig. 7Be; bl.c), the supporting cells between which bear short cilia. This latter region is short and is replaced by a glandular lining of tall, pale blue-staining cells and occasional red-staining cells (Fig. 7Bf-h; m.o) which continue through the next region of the mid-oesophagus. Torsion occurs at the commencement of the blue-staining area, the ventral groove (v.c) moving up the right side (Fig. 7Bd, e). When in a dorsal position, the squamous epithelium is replaced by red-staining gland cells like those in the anterior part of the "valve". These cells occlude the ventral groove and the radial muscles beneath the dorsal folds disappear. This narrow zone of red-staining cells persists through the next portion of the mid-oesophagus. The gland cells in the pretorsional dorsal "food groove" are replaced by a cuboidal epithelium which forms a ventral thin-walled, weakly ciliated channel. The mid-oesophagus narrows only slightly as it passes between the circum-oesophageal ganglia, and there is no appreciable change in cytology or structure behind this point for a distance equal to that which lies in front. In the next region the glandular epithelium is reduced in height and the pretorsional ventral channel is lost; correspondingly, the muscular coat, which was rather thin through the anterior part of the mid-oesophagus, suddenly increases in thickness. An irregular epithelium containing greenish-staining granules abruptly replaces the gland cells of the anterior section of this muscular region, although there is

also a narrow, ventral ciliated strip which is continuous with the dorsal food groove and is bordered by the 2, low, ciliated dorsal folds (Fig. 7E). This epithelium probably represents the anterior part of the oesophageal gland (gland of Leiblein). The muscular coat is very thick at this point and the lumen of the oesophagus rapidly narrows. An outer circular layer makes up the bulk of this coat, but there is also a thin, inner layer of longitudinal muscle. The ventral ciliated strip disappears near the posterior end of this portion of the mid-oesophagus, but the pretorsional ventral groove reappears dorsally and leads to the opening of the minute gland of Leiblein. The duct of this gland is embedded in the muscular oesophageal wall up to the posterior limit of the mid-oesophagus. The gland itself (g.l) is a short, finger-like caecum, much narrower than the mid-oesophagus although of a similar diameter to the posterior oesophagus (Fig. 7F). It is a simple tube with a very thin, outer muscular coat and is lined with irregular cells containing greenish granules of the same type normally seen in this gland, although the characteristic budding of their distal ends is rather infrequent. The lumen of the mid-oesophagus is divided into 2 by the formation of a partition where the dorsal groove is closed off to become the duct of the gland of Leiblein. The lower portion becomes ciliated and is continuous with the posterior oesophagus.

In contrast to the mid-oesophagus, the posterior oesophagus (p.oes) is very narrow and has only a thin external layer of muscle in all but its most anterior section. It has a ciliated, non-glandular, columnar epithelium and a few longitudinal ridges result from variation in the height of these cells, there being about 6 ridges initially and 4 near the stomach. The Stomach and Digestive Gland. The oesophagus becomes confluent with the stomach on its posterior side, and the intestine lies alongside. Two very short digestive gland ducts open near

the oesophageal aperture, the larger on the posterior wall leading to the large left lobe of the digestive gland, whereas the other, the duct of the small right lobe, is situated ventrally.   A short caecum forms the right (upper) part of the stomach and has tall, strongly ciliated, closely spaced ridges which run in a direction parallel to the oesophagus and intestine. Below this region, on the anterior side is the main gastric lumen with ciliated folds running from the oesophagus to the anterior gastric wall. A distinct style sac region is separated from the gastric lumen and has 2 large typhlosoles bordering a ventral groove. A small, cuticulate gastric shield projects into the gastric lumen on the anterior edge of the stomach, just behind the style sac.

A small anterior (right) lobe of the digestive gland lies in front of the stomach but most of the gland comprises the posterior (left) lobe behind. There are 2 types of digestive cell, the majority being elongate and having long cilia and variably staining granules which are mostly contained in the proximal half of the cell.   A less abundant type is very broad. These cells contain densely staining red granules and have very narrow distal ends which are not ciliated.

The Intestine and Anal Gland. There are no glandular cells in the posterior part of the intestine, this having only a ciliated columnar epithelium and a moderately wide lumen compared with the posterior oesophagus, and it narrows towards the anus. At the beginning of the rectum the epithelium becomes shorter and numerous epithelial gland cells with large, orange-staining granules occur amongst the ciliated cells. The cells take on a cuboidal form when the rectum is distended with faecal material.   The narrow distal portion of the rectum has only ciliated columnar cells and, consequently, a very narrow lumen.

The anal gland opens directly at the anus (Fig. 8D) and is a single tube with short side branches. It has a typical epithelium of irregular columnar cells containing   greenish - brown - staining granules and these aggregate in the distal ends of the cells which are then budded off.

The Male Genital System

The testis lies above the digestive gland and does not ramify into it. Sperm is stored in the swollen, convolute seminal vesicle (Fig. 8A) which is lined with squamous epithelium.   There is a very short ciliated gonopericardial canal (p.d) at the commencement of the renal vas deferens. The renal section of the vas deferens is a very narrow duct that opens into a pallial seminal groove (s.gr). This ciliated groove is formed by a flap on the lower edge of the right pallial wall which lies against the pallial floor (Fig. 8B). Two ridges, which border this groove near the base of the penis, are occupied by blue-staining subepithelial gland cells, although the epithelium is composed of only ciliated cuboidal cells.

The penis (pen) is short and thick and has a shallow, ciliated groove continuous with the sperm groove, situated on the left.   A central rod of red-staining prostatic gland cells liberates its secretion into a narrow ciliated duct that runs through them, and this opens at the distal end of the penis at the point where the penial groove terminates. A mass of sub-epithelial blue-staining gland cells are continuous with those in the anterior part of the seminal groove, and these lie amongst the connective tissue and muscle fibres comprising the bulk of the penis. The outer epithelium consists of short, ciliated cells and a few gland cells.

The Female Genital System

The Ovary and Upper Oviduct.   The large ovary contains large yolky eggs up to 400 μ in diameter and remains quite separate from the digestive gland. The upper oviduct is constructed in the same way as that of *Strigatella* and *Austromitra*.   The short, ciliated, non-

muscular renal portion passes next to the pericardial wall and there is no gonopericardial duct. A long, narrow arm of the renal organ, however, opens into the oviduct by way of a very narrow aperture. This unusual phenomenon has also been recorded in *Marginella desjardini* Marche-Machad (Graham, 1966).

The Albumen Gland and Ingesting Gland. A posterior glandular mass, the albumen gland (Fig. 8C; alb), has short cells containing red-staining granules instead of the normal blue-staining tissue. This gland is constructed in the normal fashion and the oviduct opens ventrally near its anterior end. A short, median region (Fig. 8F; c.r), with thin, slightly muscular walls which are heavily folded and lined with a ciliated cuboidal epithelium, lies between the posterior gland and the capsule gland. A considerable number of ciliated tubules (i.d) branch off from this area both dorsally and laterally, especially from the right side. These tubules are irregularly coiled and open into vesicles (i.g) lying mostly on the left side of the oviduct, although in this median region they also lie dorsally. The vesicles extend almost to the anterior and posterior extremities of the gland and usually contain small bundles of loose sperm. They are lined with large cells of very variable form and size which have pale blue, non-glandular cytoplasm and large, central nuclei. Although the vesicles are probably homologous with the ingesting gland of other stenoglossans they present a totally different appearance to those that have been described and, in addition, there is no sign of sperm ingestion. They might more appropriately be termed seminal receptacles. The ciliated tubules are lined with cuboidal cells and are not muscular.

The Capsule Gland and Anterior Structures. The capsule gland (Fig. 8E; cap) begins in front of the ciliated region, their walls being continuous. The ventral channel (v.c) which had become very subdivided in the ciliated region, retains a single fold initially but this quickly disappears until only a ciliated ventral channel remains, overlapped by a short glandular fold on either side. The walls of the capsule gland show only 2 types of glandular cells. A short posterior region stains blue and both walls are of equal thickness, whereas the remainder of the gland stains red, and the cells, which are larger than those of the posterior red-staining gland, have relatively smaller granules. In addition, the outer (right) wall is only a quarter as thick as the inner wall in this region. Near the anterior end of the capsule gland a short, ciliated right fold appears above the narrow ventral channel. Just behind the bursa copulatrix the walls of the capsule gland become thin by the shortening of the epithelial cells, although they still contain red-staining granules. The vestibule (Fig. 8D; vest) lies on the outside of the short bursa copulatrix (b.c) and has a simple ciliated epithelium. A small gonopore (Fig. 8D) is confluent with that of the bursal opening and lies just behind the anterior end of the oviduct. There is no true vaginal region apart from the ciliated lips of the gonopore.

The bursa copulatrix (b.c) is, along most of its ventral side, open to the pallial cavity. Its inner walls are lined with a non-ciliated red-staining glandular epithelium, but a thick lobe, lined with pavement epithelium and consisting of connective tissue and a few muscle fibres, projects from the right dorsal wall and nearly fills the lumen. This lobe diminishes in size and disappears before reaching either end of the bursa. Only a few muscles surround the ciliated bursal lips and the remainder of the bursa is not very muscular. No sperm were observed in the bursa in any of the specimens sectioned.

No pedal gland was found in the female, either in the living animal or in sectioned material.

MICROVOLUTA MARGINATA (Hutton)

1885 *Turricula marginata* Hutton, Trans. N. Z. Inst., 17: 315, pl. 18, fig. 4.
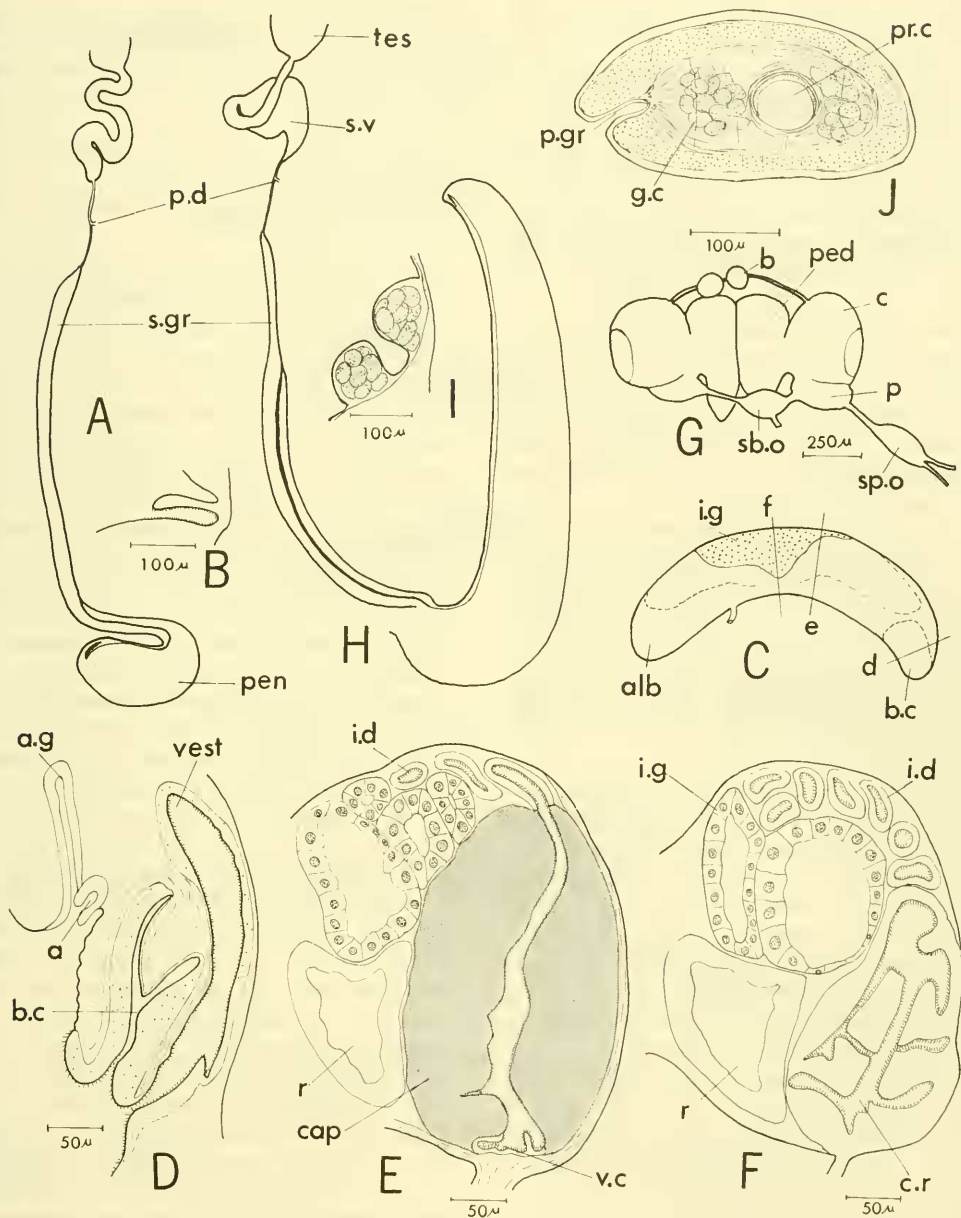1905 *Vulpecula (Pusia) biconica*; Mur-

FIG. 8. A–G. *Peculator hedleyi* (Murdoch): A. A diagram of the male genital system; B. A transverse section of the posterior part of the seminal groove; C. A diagrammatic lateral view of the pallial oviduct. The sections d–f correspond to figs. D–F; D. A transverse section of the bursa copulatrix, vagina and vestibule and showing the anus and anal gland opening; E. A transverse section of the posterior end of the pallial oviduct showing the ingesting gland and its ciliated ducts; F. A transverse section of the ciliated, median part of the pallial oviduct showing the ingesting gland; G. A diagram of the circum-oesophageal ganglia viewed dorsally with the cerebral ganglia separated and spread apart. H–J. *Microvoluta marginata* (Hutton): H. A diagram of the male genital system; I. A transverse section of the anterior part of the seminal groove. J. A transverse section through the middle region of the penis.

doch & Suter, Trans. N. Z. Inst., 38: 289, pl. 23, fig. 22.

1927 *Microvoluta   biconica*;   Finlay, Trans. N. Z. Inst., 57: 410.

1930 *Microvoluta cuvierensis* Finlay, Trans. N. Z. Inst., 61: 242, pl. 43, figs. 19, 21.

1970 *Microvoluta marginata*; Cernohorsky, Bull. Auck. Inst. Mus., 8: 122, pl. 15, figs. 14-19, pl. 16, figs. 1-2.

The radula of *Microvoluta australis* Angas is figured by Peile (1922) but no description of any aspect of the animal of *M. marginata* has previously been available.   The shell is figured in the original diagnosis by Finlay (1930), and by Cernohorsky (1970).

M. marginata lives in moderately deep to deep water (15-270 fathoms) around the coasts of New Zealand, extending to the Snares Islands and to the Chatham Islands.   The shell attains a length of about 7 mm and usually has strong axial ribs and spiral cords, although the degree and detailed pattern of sculptural development is variable.

Living specimens were obtained from several localities off the north east coast of the North Island. These were all collected by the writer on the Marine Department vessel "Ikatere" from: 25 fathoms off Bergens Point, south of Doubtless Bay; 24 fathoms off Cone Rock, Whangaroa; 85 fathoms south east of the Cavalli Islands; and 29 fathoms 4 miles west of Little Barrier Island.

The living animal is translucent white with small clusters of yellow, orange and white pigment cells on the dorsal surface of the foot.   A moderately long siphon projects from beneath the siphonal notch of the shell and has pale yellow or orange pigment cells scattered over its surface. The· eyes are about $^1/_3$ of the way along the slender tentacles which have a few yellow spots.   The foot is broad and is evenly rounded behind, with short expansions in front and a slightly indented anterior edge.   There is no opercular rudiment.

The mantle cavity is like that of *Peculator*, though it was not examined while the animal was alive. The osphradium has about 14 filaments, those on the left side being shorter. The ctenidium is relatively large, with about 30 triangular filaments.

The renal organ is like that of *Austromitra* and *Peculator*.

The Alimentary Canal

The retracted proboscis (Fig. 9F) is similar in structure and shape to that of *Peculator*, but a compact cluster of gland cells lies on each side beneath the proboscis wall (Fig. 7H; g.c). These do not extend into the dense muscle and connective tissue surrounding the buccal cavity but terminate behind at the end of the odontophore. These cells stain blue, or red, the latter type having large granules, and clearly represent a further development of the loose subepithelial gland cells seen in *Peculator*. The outer epithelium of the proboscis is ciliated dorsally and laterally but is covered with cuticle on its ventral and anterior surfaces. Unlike the situation in *Peculator* the muscles of the proboscis wall are not arranged into distinct zones but are a mixture of variously orientated fibres. A short, muscular tube lies in an invagination behind the minute mouth and is lined with very thick cuticle. This tube is attached to the proboscis wall by a dense series of short retractor muscles and the odontophore lies just behind it. Protrusion of the odontophore is probably accompanied by the eversion of this inner mouth. The weakly cuticulate oral invagination surrounding the oral tube is loosely bound to the thin, outer proboscis wall by many tangential fibres which may act as retractors and/ or dilators. There is no oral invagination or separate tube in *Peculator*.

Lying mostly within the retracted proboscis behind the oral tube is the odontophore. Massive subradular membrane retractor muscles are attached to the narrow odontophoral cartilages (od.c) while a short odontophoral retractor muscle is attached directly to their ends and ascends to the floor of the cephalic cavity. Thus there is no
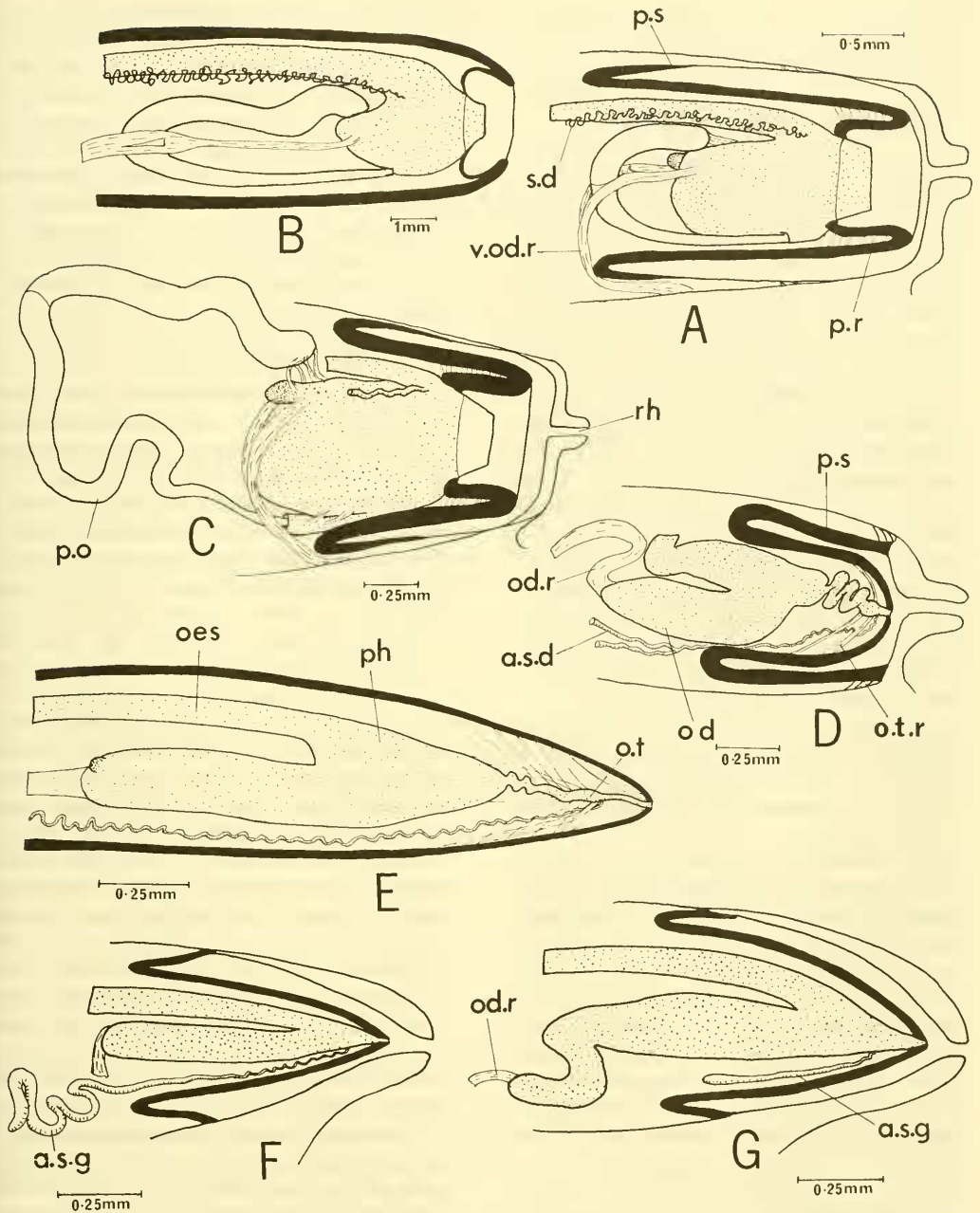
FIG. 9. Comparative diagrams of the buccal mass (shown stippled) of the mitriform gastropods to show the relationships of the main structures. The proboscis wall is solid black and the radular sac is shown densely stippled where it protrudes from the odontophoral muscles. A. *Strigatella paupercula* (Linnaeus). B. *Mitra mitra* (Linnaeus). C. *Imbricaria conovula* (Quoy and Gaimard). D. *Austromitra rubiginosa* (Hutton). E. *Vexillum plicarium* (Linnaeus). (Muscle fibres are shown running from the oral tube to the buccal mass and proboscis wall). F. *Microvoluta marginata* (Hutton). G. *Peculator hedleyi* (Murdoch).

development of the elongate muscular rod seen in *Peculator*. The radula is very similar to that of *Peculator* except that the lateral teeth are relatively larger and a little heavier.

The single accessory salivary gland (Fig. 9F; a.s.g) is longer than in *Peculator* as it commences opposite the valve of Leiblein. Its coiled duct (Fig. 7H; a.s.d) opens just in front of the odontophore after passing below it as a minute tube. A short posterior portion about 60 μ wide has a wall consisting of thin layers of inner circular, and outer longitudinal muscles, and an inner epithelium of small, irregular, pale bluish-staining gland cells with granular contents. A similar type of cell forms a single layer outside the muscular tube a little further anteriorly where the tube reduces in width. At the same time the inner epithelium becomes more pronounced, but at the base of the proboscis the glandular epithelium is replaced by squamous cells and the tube becomes very narrow.

The buccal cavity, anterior, mid- and posterior oesophagus are like those of *Peculator* and, although the salivary glands are rather larger, they have the same structure.

The stomach differs from that of *Peculator* in not having a definite caecum, although the posterior part is expanded. The style sac is especially well-developed with the typhlosole on the anterior wall being mainly composed of large, blue-staining gland cells. The digestive gland, rectum and anal gland are like those of *Peculator*. Fine mineral particles, diatom cases and spicule-like fragments have been seen in the faecal material.

The Male Genital System

There are few differences from the system described in *Peculator*. The seminal groove (Fig. 8H; s.gr) is shorter and is replaced about halfway along the pallial cavity by glandular ridges (Fig. 8I) similar to those situated further in front in *Peculator*. The penis is much longer than in *Peculator* although there is a similar penial groove (Fig. 8J; p.gr) and a central rod of prostatic tissue (pr.c). The prostatic tissue is surrounded by a ring of circular muscle and a ciliated prostatic duct opens distally at the end of the seminal groove as it does in *Peculator*. Two lateral tracts of blue-staining cells (g.c) lie on either side of the prostatic mass, and the outer penial epithelium is ciliated and contains abundant mucous cells.

The Female Genital System

Only a single female was available for examination and although the general features of the female system resemble those of *Peculator*, no detailed comparison could be made. The ovary is like that of *Peculator* but the albumen gland cells stain blue and are very short, being only 20-30 μ in height. The gland also has a wide lumen and is of an irregular shape. Between the albumen and capsule glands the ciliated sac is found, but in this species it is smaller than in *Peculator* and is clearly just a swelling of the ventral channel. Only 2 non-muscular, ciliated ducts are given off from this area and both open into the "ingesting gland" or seminal receptacles. These vesicles have the same cytological structure as those in *Peculator*. Long cilia in the ducts mould sperm into coherent masses which are visible in the lumen of the vesicles, but no indication of sperm ingestion was observed. The capsule gland appears to be similar to that of *Peculator* but no detailed observations were possible. A short, ciliated fold lies on the left of the ventral channel in the anterior part of the capsule gland. A thin-walled vestibule is on the right of the bursa copulatrix. This is lined with mucous cells and opens into a wide, muscular vagina which extends along the anterior half of the bursa to open distally alongside the bursal opening. The vagina has an orange-staining cuboidal epithelium which bears long cilia.

The bursa copulatrix has a thick wall

of circular muscle and its interior is irregularly folded. Although the bursal opening is ciliated the remainder is lined with columnar cells about 18 μ in height which are covered with a "soft" cuticle. The differences in the anterior female genital structures of *Peculator* and *Microvoluta* can, no doubt, be attributed to the relative size of the penis in these 2 species.

As in *Peculator* there was no indication of a pedal gland. Single egg capsules have been observed attached to the dorsal or lateral surfaces of the shells of a few specimens of *Microvoluta*. Each capsule consists of rather fragile, transparent, horny material and is about 0.7 mm in diameter. The capsules are hemispherical in shape and a single embryo develops within each. When emergence takes place the crawling juvenile breaks away most of the top of its capsule.

DISCUSSION

There is a general uniformity in the shells of mitriform neogastropods that has resulted in considerable difficulty in placing them in genera and higher taxa. Most of the mitriform species have solid shells with rather elongate apertures which are ornamented with columellar plaits, and no operculum. Various authors have shown that despite the similarity of their shells, the mitriform gastropods fall into several well defined groups based upon radular pattern. Risbec (1928) found that the anatomy of several species also showed considerable differences and Thiele (1929), presumably using this work as a basis, listed the anatomical characters of each of his subfamilies and arrived at the following classification:

Superfamily Volutacea
  Family Mitridae
    Subfamily Mitrinae(*Mitra, Imbricaria*)
    Subfamily Vexillinae (*Pusia, Vexillum*)
    Subfamily Cylindrinae (*Cylindra*)

Thiele further suggested that the structure of the anterior alimentary canal is so different that 2 families, Vexillidae and Mitridae, should probably be distinguished. Risbec (1955) arranged the species he investigated into several different families. The true mitrids he aligned with the Toxoglossa, as he suggested that the epiproboscis (poison gland) is homologous with the toxoglossan poison gland. His arrangement was as follows:

Suborder Toxoglossa
  Superfamily Mitracea
    Family Mitridae
      Subfamily Mitrinae (*Mitra, Strigatella*)
      Subfamily Cylindrinae (*Cylindra*)
Suborder Stenoglossa
  Superfamily Muricacea
    Family Purpuridae
      "new subfamily" (*Pusia*)
  Superfamily Buccinacea
    Family Nassidae
      "new subfamily" (*Vexillum*)

This classification has been subsequently accepted only by Taylor & Sohl (1962) who used it in their summary of gastropod classification.

The next major attempt to classify the family Mitridae was that of Cernohorsky (1966) which was based primarily on radular and shell features. This author made no reference to Risbec's work and used the same scheme as Thiele except for the use of an additional sub-family, Imbricariinae. Cernohorsky's scheme is summarised below:[3]

---

[3]Since the above account was prepared Cernohorsky (1970) has published a comprehensive review of the "Mitridae and Volutomitridae". The classification that he adopts is essentially that of his earlier (1966) work.

Superfamily Volutacea
  Family Mitridae
    Subfamily Mitrinae (*Mitra*, *Stri-gatella*, *Neocancilla*, *Charitodoron*)
    Subfamily Imbricariinae (*Imbricaria*, *Cancilla*, *Scabricola*, *Swainsonia*)
    Subfamily Vexillinae (*Vexillum*, *Pusia*, *Austromitra*)
    Subfamily Cylindromitrinae (*Pterygia* = *Cylindra*)

Azuma (1965) raised the Vexillinae to family rank because of its radular characters.

A small group of species around *Volutomitra* have been variously placed in the Volutidae (Powell, 1951) or in the subfamily Volutomitrinae of the Volutidae (Thiele, 1929; Smith, 1942; Cernohorsky, 1966) and in the Mitridae (Cotton, 1957; Powell, 1962). It appears that *Microvoluta* and *Peculator* belong in this group so that the families Microvolutidae and Peculatoridae erected by Iredale & McMichael (1962) are synonyms.

The present investigation suggests an arrangement that is not entirely in accordance with any of the previous schemes. Of the species examined there appear to be 3 very distinct groups; the true mitrids (*Strigatella*, *Mitra*, *Imbricaria*); the "*Vexillum* group" (*Vexillum*, *Austromitra*); and the "*Volutomitra* group" (*Microvoluta*, *Peculator*). Anatomical differentiation between each of these groups, particularly in the alimentary canal, is so marked that their separation at the family level appears to be fully justified. There do not appear to be sufficient differences to separate *Imbricaria* from the true mitrids, even at the subfamily level. Cernohorsky (1966) does not indicate how the Imbricariinae can be separated from the Mitrinae. The radula, shell features and anatomy of the Cylindromitrinae indicate that this group is related to the Mitrinae and for the present should be regarded as a subfamily of the Mitridae.

The Volutomitridae has generally been associated with the Volutidae because of the similarity of the radular teeth of *Volutomitra* and *Scaphella* species. This resemblance is only superficial as the shells and the morphology of the animals have very few features in common. Sars (1878) has described the radula and the gross features of the proboscis of *Volutomitra grønlandica* (Beck), the type of that genus, and these structures very closely resemble those of *Microvoluta* and *Peculator*. Peile (1922) described the radula of *Microvoluta australis* Angas, the type species of *Microvoluta*, and states that there are no lateral teeth, whereas all other members of the family, including *Paradmete* (see Thiele, 1929; Powell, 1951) have these teeth. The radula of the type species of *Peculator*, *P. verconis* Iredale, is unknown. Probably some generic rearrangement is require to take the radular features into account, but more species should first be examined.

The anatomy of a species of *Pusia* was described by Risbec (1928) and his description of the shell suggests that it was *P. consanguinea* (Reeve) rather than the closely allied *P. microzonias*, the type species of the genus. The central tooth of the radula has only 3 cusps but otherwise it is similar to that of *Vexillum* and *Austromitra* species and the alimentary canal is also similar. It would thus appear that *Pusia* and *Vexillum* are related genera and can be placed together in 1 family. Risbec (1955) suggested *Pusia* be placed in the Nassariidae, a decision with which the writer finds no merit whatsoever.

The scheme adopted here for the classification of the mitriform gastropods can be summarised as follows:
  Family Mitridae
    Subfamily Mitrinae (=Imbricariinae)
    Subfamily Cylindromitrinae
  Family Vexillidae
  Family Volutomitridae (=Microvolutidae, Peculatoridae)

A synopsis of the chief distinguishing features of the 3 families is given in

tabular form below (Table 3). The main differences between the Mitrinae and the Cylindromitrinae are given in Table 4. The anatomical data on the Cylindromitrinae are obtained from Risbec's (1928) account of the anatomy of *Pterygia crenulata*.

The whole question of the relationships of the families of the Neogastropoda will be discussed elsewhere, but there can be little doubt that the 3 groupings suggested here are of family level. The morphological characters show a level of differentiation similar to or greater than that seen in other neogastropod family groups.

Despite the considerable differences in the alimentary canal between the Mitridae and the Vexillidae, their reproductive and nervous systems are generally similar which may suggest a close relationship. Both the male and female genital systems of the volutomitrids *Microvoluta* and *Peculator*, however, show considerable differences from those of the other 2 families. There are some common features of the alimentary canal between the Vexillidae and the Volutomitridae. They both have a gland of Leiblein, a glandular mid-oesophagus, a valve of Leiblein and accessory salivary glands. These features, however, are found in many neogastropod families and do not necessarily indicate a close relationship. Graham (1941) has suggested that a different position of torsion in the mid-oesophagus indicates a different origin. In the Vexillidae the torsion of the alimentary canal seems to occur just behind the nerve ring whereas in the Mitridae it probably takes place near the position of the valve of Leiblein. Torsion in the Volutomitridae occurs on the posterior side of the valve of Leiblein but in front of the nerve ring. Thus, on this evidence alone, the 3 families are well separated.

The renal organ in the Mitridae is like that of the Olividae (Marcus & Marcus, 1959) and the Volutidae (Perrier, 1889) in having the primary and secondary renal lamellae separated into 2 distinct glandular areas, whereas in the Vexillidae and the Volutomitridae these 2 types of lamellae are interwoven as in *Buccinum* (Perrier, 1889; Dakin, 1912) and *Nucella* (Perrier, 1889; Fretter & Graham, 1962).

The ability of the Mitridae to secrete a purple hypobranchial fluid similar to that seen in the Muricidae and the Volutidae is not shared by the Vexillidae or the Volutomitridae, but does occur in some Terebridae. When more information is available, egg capsules may prove to have a consistently distinctive form for each of the families.

Although the Mitridae resembles the Buccinidae and its allied families in the absence of accessory salivary glands, the reduction or absence of a valve of Leiblein, and the multicuspid lateral teeth of the radula, the presence of a purple hypobranchial secretion and an anal gland suggest affinity with either the Muricidae or the Volutidae. Other features of the family such as the columellar plaits of the shell, the absence of an operculum, and the very elongate proboscis, fit the Volutidae better than the Muricidae. A long proboscis is also found in the Buccinidae and related families.

One of the most puzzling questions concerning the Mitridae is how the epiproboscis was evolved. Probably this was brought about by an elaboration of a trend towards the ventral migration of the salivary ducts, such as that seen in the Vexillidae. As the buccal mass lies just behind the mouth, this may have resulted in the openings of these ducts being pushed to the edge of the mouth. Eventually these may have been placed on a small papilla, but the advantages of this are not known. Invagination of this papilla would probably accompany its further elongation. The salivary glands have a second type of secretory cell not seen in the Vexillidae or the Microvolutidae and it is possible that these cells are responsible for the production of a toxic substance. It is quite

TABLE 3. The chief distinguishing features of the 3 families of mitriform gastropods.

Feature	MITRIDAE	VEXILLIDAE	VOLUTOMITRIDAE
Shell			
Size	large to medium	large to small	medium to small
Predominant sculpture	smooth or spiral	axial	smooth or axial
Radula			
Lateral teeth	usually multicuspid or absent	simple, curved	needle-like or absent
Central teeth	usually relatively small, multicuspid	relatively large, 3 or more cusps	relatively large, 1 cusp, long basal processes
Hypobranchial secretion	purple	yellow-green	colourless
Alimentary canal			
Proboscis	long	moderately long or short	short
Epiproboscis	present	absent	absent
Mouth	large, with peristomal rim	small, no peristomal rim	small, no peristomal rim
Oral tube	absent	long	very short or absent
Accessory salivary glands	absent	large, paired	small, single
Salivary ducts	free or in oeso-phageal wall	in oesophageal wall	in oesophageal wall
Valve of Leiblein	small or absent	large	large
Region of torsion	valve of Leiblein (?)	behind nerve ring	behind valve of Leiblein but in front of nerve ring
Gland of Leiblein	absent	moderately large or small	very small, only parti-ally separated from oesophagus
Mid-oesophagus	very short, not con-spicuously glandular	moderately short or long, glandular	very long, glandular
Stomach	often with muscular gizzard, a modified style sac and no caecum	simple, with short posterior caecum and style sac	with style sac and gastric shield, with or without caecum
Genital system			
Gonad	tubules intermingle with digestive gland	tubules separate from digestive gland	tubules separate from digestive gland

Table 3 (continued)

Feature	MITRIDAE	VEXILLIDAE	VOLUTOMITRIDAE
Ingesting gland or seminal receptacle	cells columnar, ingest sperm and yolk	cells columnar, ingest sperm	cells cuboidal, no sperm ingestion
Pedal gland	present	absent	absent
Egg capsules	vase-shaped	inverted hemispherical (*Austromitra*)	hemispherical (*Microvoluta*)
Prostate gland	large pallial gland, closed except for small posterior pallial opening	large pallial gland, closed except for small posterior pallial opening	open pallial groove, prostatic tissue in penis
Renal organ	primary and secondary lamellae interdigitate	primary and secondary lamellae separate	primary and secondary lamellae separate

possible that a more primitive member of the Mitridae exists which may give a definite indication of the evolution of this organ.

Maes (1971) has shown in *Mitra nodulosa* (Gmelin) that the epiproboscis deposits the toxin against the soft parts of the prey and that the toxin permeates unbroken epidermis (presumably killing the prey).

The structure of the mid-oesophagus in the Volutomitridae is different from that of any other neogastropods that have been described. It has the oesophageal gland (gland of Leiblein) apparently only partially separated from the mid-oesophagus, the anterior portion being incorporated in the oesophagus itself. Thus the gland was probably partially separated from the oesophagus from behind forwards. There is, however, no trace of any ventral folds in the gland to confirm this supposition. The gland of Leiblein in the remainder of the neogastropods was, as shown by Graham (1941), removed backwards from the mid-oesophagus and then turned over so that its dorsal surface, along which run the ventral (oesophageal) folds, lies immediately above the oesophagus. The glandular area behind the valve of Leiblein in the volutomitrids represents a secondarily elongated part of the mid-oesophagus from which the oesophageal gland retreated. This part appears to have been largely pulled through the nerve ring so that the area where torsion occurs lies just behind the valve of Leiblein.

Cernohorsky (1965, 1966) suggests that the Mitridae feed on micro-organisms grazed or swept from surface detritus, and that the Vexillidae feed on dead or living flesh. The gut contents of the animals described above indicate that *Strigatella* and *Imbricaria* feed on sipunculids and molluscs, although they may well feed on other animals, and *Austromitra* has been observed feeding on ascidians. The faecal residue of *Microvoluta* shows only fine particulate material that could have been derived from the accidental inclusion of detritus while feeding, or from the gut contents of its prey. The food of *Strigatella*, *Imbricaria* and presumabley *Mitra* is swallowed in chunks that are stored in the crop region and then triturated by the muscular gizzard of the stomach. *Vexillum* and *Austromitra* appear to be adapted for swallowing small pieces of food which are then moved rapidly to the mid-oesophagus and are broken down by the digestive juices secreted by the

TABLE 4. The main differences between the 2 subfamilies, Mitrinae and Cylindromitrinae

Feature	MITRINAE	CYLINDROMITRINAE
Shell	variable in outline, often elongate	cylindrical, with depressed spire
Radular formula	1–1–1	0–1–0
Head-foot	small in relation to shell	large in relation to shell
Alimentary canal		
Proboscis	long, rather broad	very long, narrow
Epiproboscis	moderately large in relation to the powerful buccal mass	very large in relation to the minute buccal mass
Salivary ducts	free from oesophageal wall	apparently within wall of oesophagus
Stomach	with muscular gizzard in oesophageal region	apparently no muscular region

gland of Leiblein and possibly the mid-oesophageal glands. Cernohorsky (1965) has observed *Vexillum* species enveloping prey with the foot after the manner of some Olividae. The Volutomitridae probably scrape particles of flesh or may even feed on body fluids which are sucked into the proboscis by the powerful buccal walls. Again preliminary breakdown of food may occur by a secretion from the mid-oesophageal glands, but in addition some of the epithelium of the gland of Leiblein is in direct contact with the food as this epithelium is incorporated in the oesophagus. Possibly a protostyle is sometimes formed in the style sac, which may account for the retention of that part of the stomach, and for the presence of a gastric shield.

Raeihle (1969) has shown that *Thala floridana* (Dall) feeds on a variety of gastropods which it kills by a sting from its extended proboscis. Cernohorsky (1970) also notes an observation (but does not give a source) of a species of *Thala* "killing another mollusc with the extendable poison gland". This genus has a vexillid type of radula and shell and may eventually prove to be an atypical mitrid when anatomical information is available.

Risbec (1955) has noted the advantage of columellar plaits in providing "slip free traction" for the columellar muscle. This shell feature has been evolved independently in many groups including, within the Neogastropoda, the Volutidae, Olividae, Fasciolariidae, Turridae (Borsoniinae), Marginellidae and the Turbinellidae, and may well have evolved separately in the 3 families of mitriform gastropods.

LITERATURE CITED

AZUMA, M., 1965, On the radulae of the family Vexillidae. *Venus*, 24: 53-57.

BARNARD, K. H., 1959, Contributions to the knowledge of South African marine Mollusca. Pt. 2. Gastropoda: Prosobranchiata: Rachiglossa. *Ann. S. Afr. Mus.*, 55(1): 1-237.

CARRIKER, M. R., 1943, On the structure and function of the proboscis in the common oyster drill, *Urosalpinx cinerea* Say. *J. Morph.*, 73: 441-506.

CATE, J. M., 1967, The radulae of nine species of Mitridae. *Veliger*, 10(2): 192-195.

CATE, J. M., 1968, Mating behaviour in *Mitridae* Melvill, 1893. *Veliger*, 10(3): 247-252.

CERNOHORSKY, W. O., 1965, The Mitridae of Fiji. *Veliger*, 8(2): 70-160.

CERNOHORSKY, W. O., 1966, A study of mitrid radulae and a tentative generic arrangement of the family Mitridae. *Veliger*, 9(2): 101-126.

CERNOHORSKY, W. O., 1970, Systematics of the families Mitridae and Volutomitridae (Mollusca: Gastropoda). *Bull. Auckland Inst. Mus.*, 8: 1-190.

COAN, E., 1966, Nomenclatural units in the gastropod family Mitridae. *Veliger*, 9(2): 127-137.

COOKE, A. H., 1920, The radulae of the Mitridae. *Proc. zool. Soc. London* 29: 405-422.

COTTON, B. C., 1957, Family Mitridae. *Roy. soc. S. Austr., Malacol. Sect., Publ.* 12. 7 p.

CROSS, E. R., 1967, Meet *Mitra papalis* (Linnaeus). *Hawaiian Shell News*, 15 (4): 7.

DAKIN, W. J., 1912, *Buccinum* (the whelk). *L.M.B.C. Mem.* 20, London, Williams and Norgate.

FINLAY, H. J., 1930, Additions to the Recent molluscan fauna of New Zealand. *Trans. N. Z. Inst.*, 61: 222-247.

FRETTER, V., 1941, The genital ducts of some British stenoglossan prosobranchs. *J. mar. biol. Ass. U. K.*, 25: 173-211.

FRETTER, V., 1946, The pedal sucker and anal gland of some British Stenoglossa. *Proc. malacol. Soc. Lond.*, 27: 126-130.

FRETTER, V., & GRAHAM, A., 1962, *British prosobranch molluscs, their functional anatomy and ecology*. Ray Soc., London.

GRAHAM, A., 1941, The oesophagus of the stenoglossan prosobranchs. *Proc. Roy. Soc. Edinb.* B, 61: 1-23.

GRAHAM, A., 1966, The fore-gut of some marginellid and cancellariid prosobranchs. *Stud. trop. oceanogr.*, Miami, 4(1): 134-151.

HABE, T., 1944, Eggs and larvae of some marine gastropods found in Japan. *Venus*, 13: 187-201.

IREDALE, T. & McMICHAEL, D. F., 1962, A reference list of the marine Mollusca of New South Wales. *Mem. Aust. Mus.*, 11: 1-109.

MAES, V. O., 1971, Evolution of the toxoglossate radula and methods of envenomation. *Amer. malacol. Union, Ann. Reps.* 1970: 69-72.

MARCUS, E. & MARCUS, E., 1959, Studies on 'Olividae'. *Bolm. Fac. Filos. Ciên. Univ. S. Paulo*, 232, *Zool.*, 22: 99-188.

MORTON, J. M. & MILLER, M. C., 1968, *The New Zealand sea shore*. Collins, London. 638 p.

OSTERGAARD, J. M., 1950, Spawning and development of some Hawaiian marine gastropods. *Pacific Sci.*, 4: 75-115.

PANTIN, C. F. A., 1962, *Notes on microscopical technique for zoologists*. Cambridge Univ. Press.

PEILE, A. J., 1922, The radulae of some Mitridae. *Proc. malacol. Soc. Lond.*, 15: 93–94.

PEILE, A. J., 1936, Radula notes. *Proc. malacol. Soc. Lond.*, 22: 139–144.

PEILE, A. J., 1937, Radula notes II. *Proc. malacol. Soc. Lond.*, 22: 181–186.

PERRIER, M.R., 1889, Recherches sur l'anatomie et l'histologie du rien des Gastéropodes Prosobranches. *Ann. Sci. natur. (Zool.)*, (7), 8: 61–315.

PONDER, W. F., 1970, The morphology of *Alcithoe arabica* (Mollusca: Volutidae). *Malacol. Rev.*, 3: 127–165.

POWELL, A. W. B., 1951, Antarctic and Subantarctic Mollusca: Pelecypoda and Gastropoda. *Discov. Rept.*, 26: 47–196.

POWELL, A. W. B., 1962, *Shells of New Zealand*, Whitcombe & Tombs, Christchurch.

QUOY, J. R. & GAIMARD, J. P., 1833, *Voyage de la Corvette l'Astrolabe*. Zoologie, 2(1): 321–686. Paris.

RAEIHLE, D., 1969, Notes on captive *Cerithium variabile* C. B. Adams and *Mitra floridana* Dall. *Amer. malacol. Union, ann. Reps.*, 1970: 35–36.

RISBEC, J., 1928, Contribution à l'étude anatomique de quelques espèces de Mitres de la presqu'île de Nouméa. *Bull. Mus. natn. Hist. nat.*, Paris, 34: 105–112, 173–180, 225–227.

RISBEC, J., 1955, Considérations sur l'anatomie comparée et la classification des Gastéropodes Prosobranches. *J. Conch.* (Paris), 95(2): 45–82.

SARS, G. O., 1878, Mollusca regionis arcticae norwegiae. *Bidrag til Kundskaben om Norges Arktiske Fauna*. Christiana. 1: 1–466.

SMITH, E. H., 1967, The neogastropod stomach, with notes on the digestive diverticula and intestine. *Trans. roy. Soc. Edinb.* 67(2): 23–42.

SMITH, M., 1942, *A review of the Volutidae*. Ann Arbor (Edwards Bro.) 70 pp.

TAYLOR, D. W. & SOHL, N. F., 1962, An outline of gastropod classification. *Malacologia*, 1(1): 7–32.

THIELE, J., 1929 (-1935), *Handbuch der systematischen Weichtierkunde*. Jena. Pt. 1: 1–376.

TROSCHEL, F. H., 1856–1893, *Das Gebiss der Schnecken zur Begründung einer natürlichen Classification*. Vol. 2. Berlin. (Rachiglossa, 1868–1869).

VAYSSIERE, A., 1901, Etude Zoologique et anatomique de la *Mitra zonata* Marryatt. *J. Conch.* (Paris), 49(2): 77–95.

VAYSSIERE, A., 1912, Observations faites sur un *Mitra zonata* vivant. *J. Conch.* (Paris), 60(4): 323–327.

WU, S.-K., 1965, Comparative functional studies of the digestive system of the muricid gastropods *Drupa ricina* and *Morula granulata*. *Malacologia*, 3(2): 211–233.

ZUSAMMENFASSUNG

DIE MORPHOLOGIE EINIGER MITRIFORMER GASTROPODEN UNTER
BESONDERER BERÜCKSICHTIGUNG IHRES VERDAUUNGS-
UND GESCHLECHTSAPPARATTS (NEOGASTROPODA)

W. F. Ponder

Verdauungskanal und Geschlechtsapparat von *Strigatella paupercula* (Linnaeus), *Austromitra rubiginosa* (Hutton) und *Peculator hedleyi* (Murdoch) werden ausführlich beschrieben und mit denen einiger verwandter Arten verglichen. Die hauptsächlichen Merkmale von Kopf, Fuss, Mantelhöhle, Nieren und Schlundring-Ganglien werden kurz angegeben.

Die Arten gehören zu 3 Familien, den Mitridae, Vexillidae und Volutomitridae, wobei jede Familie einen besonderen Typus des Verdauungskanals aufweist. Eine besondere Epiproboscis an der Proboscis der Mitridae dient als Träger der Speichelgänge. Zusätzliche Speicheldrüsen und eine Leibleinsche Drüse sind bei den Vexilli-

dae und Volutomitridae vorhanden, fehlen aber beide in den Mitridae. Während der Verdauungskanal der Vexillidae und Volutomitridae manche Züge gemeinsam haben, sind ihre Geschlechtswege ganz verschieden. Die Geschlechtsapparate der Vexillidae und Mitridae sind sehr ähnlich. Gemeinsame Merkmale der besprochenen Arten sind u.a. eine Analdrüse, Columellarfalten und Fehlen eines Operculums, ebenso eine allgemeine Ähnlichkeit der Schalen, welche Ähnlichkeiten der Autor für weniger aus- schlaggebend für die Beurteilung der Verwandtschaft der Familien hält. Andere Merkmale der Mitridae (s.s.), die bei den anderen 2 Familien nicht vorkommen sind eine hypobranchiale Purpursekretion, vasenförmige Eikapseln und eine ventrale Fussdrüse bei den Weibchen. Die Eikapseln von *Austromitra* und *Microvoluta* sind halbkugelig. Die Niere der Mitridae hat die primären und sekundären Lamellen an getrennten Stellen, sie greifen bei den anderen 2 Familien ineinander. Es scheinen keine wesentlichen Unterschiede der Schlundringganglien der 3 Gruppen zu bestehen.

H. Z.

RÉSUMÉ

LA MORPHOLOGIE DE QUELQUES GASTÉROPODES MITRIFORMES
AVEC RÉFÉRENCE SPÉCIALE À LEUR APPAREIL
DIGESTIF ET REPRODUCTEUR (NÉOGASTROPODA)

W. F. Ponder

Les appareils digestif et reproducteur de *Strigatella paupercula* (L.), *Austromitra rubiginosa* (Hutton) et *Peculator hedleyi* (Murdoch) sont décrits en détail et comparés à ceux de plusieurs espèces voisines. Les principaux caractères de la tête et du pied, de la cavité palléale, du rein et des ganglions périoesophagiens sont brièvement indiqués.

Les espèces décrites se rapportent à 3 familles, les Mitridae, Vexillidae et Voluto- mitridae, chaque famille ayant un type distinctif d'appareil digestif. Un épiproboscis particulier, présent dans le proboscis des Mitridae, sert de véhicule aux conduits salivaires. Des glandes salivaires accessoires et une glande de Leiblein se rencon- trent chez les Vexillidae et les Volutomitridae, mais sont toutes deux absentes chez les Mitridae. Tandis que les appareils digestifs des Vexillidae et des Volutomitridae ont plusieurs traits communs, leurs tractus génitaux sont tout à fait distincts. Les structures de l'appareil reproducteur des Vexillidae et des Mitridae sont très sem- blables. Les traits communs des espèces considérées sont: glande anale, plis colu- mellaires et absence d'opercule, ainsi que similarité générale de leur coquille, caractères que l'auteur considère comme d'importance secondaire, vu qu'il évalue leur parenté au niveau de la famille. D'autres caractères des Mitridae (s.s.), non rencontrés dans les 2 autres familles, comprend une sécrétion pourpre hypobranchiale, des capsules ovigères en forme de vase et une glande pédiale ventrale chez les femelles. Les capsules ovigères d'*Austromitra* et *Microvoluta* sont hémisphériques. Le rein a des lamelles primaires et secondaires nettement séparées chez les Mitridae, mais elles sont interdigitées chez les 2 autres familles. Il ne semble pas y avoir de dif- férence significative entre les ganglions circum-oesophagiens des 3 groupes.

A. L.

RESUMEN

MORFOLOGIA DE ALGUNOS NEOGASTROPODA MITRIFORMES CON
REFERENCIA ESPECIAL A SUS SISTEMAS DIGESTIVO Y REPRODUCTOR

W. F. Ponder

El canal alimenticio y sistema reproductor en *Strigatella paupercula* (L.), *Austromita rubiginosa* (Hutton) y *Peculator hedleyi* (Murdoch), se describe y e se com- para en detalle, con aquellos de otras especies aliadas. Se indican brevemente los

aspectos principales de la cabeza, pié, cavidad paleal, órganos renales y ganglios circunesofágicos.

Las especies así descriptas pertenecen a tres familias: Mitridae, Vexillidae y Volutomitridae, cada una con un tipo de canal alimenticio distinto. Una epiproboscis peculiar, presente en la proboscis de los Mitridae, sirve de vehículo a los conductos salivares. Glándulas salivares accesorias aparecen, así como una glándula de Leiblein, en los Vexillidae y Volutomitridae, pero estan ausentes en los Mitridae. Aunque el canal alimenticio en Vexillidae y Volutomitridae tienen muchos aspectos comunes sus conductos genitales son muy distintos. Caracteres comunes a las especies consideradas incluyen una glándula anal, placas columelares, y ausencia de opérculo, así como similaridad general en las conchas que el autor considera de importancia secundaria en la apreciación de las relaciones al nivel de familia. Otros caracteres de los Mitridae (s.s.) que no se encuentran en las otras familias son: secreción hipobranquial purpúrea, cápsulas ovígeras vasiformes, y una glándula pedal ventral en las hembras. Las cápsulas ovígeras de *Austromitra* y *Microvoluta* son esféricas. El órgano renal tiene las lamelas primarias y secundarias en areas separadas en los Mitridae, pero son interdigitadas en las otras dos familias. Los ganglios circunesofágicos en los tres grupos parecen no tener diferencias de significación.

<div align="right">J. J. P.</div>

АБСТРАКТ

МОРФОЛОГИЯ НЕКОТОРЫХ МИТРИДООБРАЗНЫХ GASTROPODA (NEOGASTROPODA), ОСОБЕННО ИХ ПИЩЕВАРИТЕЛЬНОЙ И ПОЛОВОЙ СИСТЕМ

В.Ф. ПОНДЕР

Детально описывается строение пищеварительной и половой систем у *Strigatella paupercula* (L.), *Austromitra rubignosa* (Hutton) и *Peculator hedleyi* (Murdoch) и проводится их сравнение с некоторыми близкими видами. Вкратце приводится описание основных черт строения области голова-нога, мантийной полости, почечного органа и вокругглоточного ганглия. Рассмотренные виды относятся к трем семействам - Mitridae, Vexillidae и Volutomitridae. Виды каждого семейства имеют различный тип строения пищеварительного канала. Особый epiproboscis, имеющийся на proboscis Митрид служит путепроводом для слюнных протоков. Дополнительные слюнные железы и железа Леблейна имеются у Vexillidae и Volutomitridae, но отсутствуют у Митрид. В то время, как пищеварительная система у Vexillidae и Volutomitridae имеют некоторые общие черты, строение их половых протоков совершенно различно. Строение половой системы у Vexillidae и Mitridae очень сходно. Общим для них является наличие анальной железы, колюмеиллярных складок и отсутсвие operculum, а также имеется сходство в общем строении их раковин. Эти признаки считаются второстепенными при установлении их родственных связей на уровне семейства. Другие признаки Mitridae (s.s.), не найденные у двух других семейств, - это гипобранхиальная секреция пурпура, вазообразные яйцевые капсулы и (у самок) наличие с брюшной стороны ножной железы. Яйцевые капсулы у *Austromitra* и *Microvoluta* - полусферические. Почечный орган у Mitridae имеет раздельные первичную и вторичную пластинки, в то время, как у двух других семейств они имеют пальцевидные выросты. Видимо, никаких значительных различий у всех трех групп в строении вокругглоточного ганглия нет.

<div align="right">Z. A. F.</div>